UNIVERSITY OF ALBERTA

Vegetation, Livestock and Waterfowl Responses to Hydrologic Gradients in Created Wetlands of the Dry Mixed Grass Prairie

by ©

Stephen Appiah Asamoah

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ABSTRACT

Declining Pintail (*Anas acuta*) populations in Canada's Prairies have been linked with crop agriculture, drought, and associated habitat loss. Although created wetlands may enhance breeding and nesting opportunities, artificial flooding may change desirable spikerush (*Eleocharis palustris*) communities to undesirable monotypic stands of cattail (*Typha latifolia*). Using greenhouse and field studies, this research examined the likelihood of using various flooding regimes to control cattail in affected wetlands, as well as enhance and/or restore spikerush in new and established wetlands.

An initial greenhouse study indicated that unlike spikerush, cattail was highly tolerant of moisture stress, with soil moisture below 5% required to induce rhizome mortality. Field studies indicated that new wetlands flooded annually in fall or spring had greater forage production and quality, primarily due to spikerush enhancement at lower elevations, which led to greater cattle foraging. Landscape impacts of flooding also extended into adjacent uplands. Pintail and other species of waterfowl favored created wetlands, with the most Pintail under spring flooding.

A parallel study assessed the effects of flood cessation on forage, plant community and waterfowl use dynamics within wetlands previously dominated by cattail. While a change in seasonality of flooding from fall to spring had limited impacts, flood cessation for up to two years reduced waterfowl abundance and forage availability, and markedly altered wetland vegetation. Species diversity increased with drying, largely due to cattail decline and the release of invasive forbs. However, cattail reductions were only temporary, likely limited by soil moisture levels that remained above 5% during the

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study. While grazing affected many forage species, these effects depended heavily on flood regime and topographic position as well.

Overall, long-term strategies to prevent plant community succession to cattail should likely include cycles of flooding with intermittent flood cessation in new wetlands, while extended drying appears necessary to achieve significant cattail control on established wetlands.

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LIST OF SYMBOLS, NOMENCLATURE & ABBREVIATIONS

1YNF – One Year of No Flooding
2YNF – Two Years of No Flooding
ADF – Acid Detergent Fiber
ANCOVA – Analysis of Covariance
ANOVA – Analysis of Variance
CF – Continuous Flooding
CP – Crude Protein
CPY – Crude Protein Yield
CWP – Contra-Costa Wetlands Project
DM – Dry Matter
DMP – Dry Mixed Grass Prairie
DPC – Desired Plant Community
DS – Drought Stress
DUC – Ducks Unlimited Canada
EID – Eastern Irrigation District
FC – Field Capacity
FF – Fall Flooding
GPS – Global Positioning System
IBB – Indicator Breeding Bird
IBWA – Indicated Breeding Waterfowl Abundance
Introduced Species – All naturalized species, weeds and exotic invaders in the DMP
IWWR – Institute for Wetland and Waterfowl Research
KWP – Kitsim Wetlands Project
LLD – Live Leaf Density
MCH – Maximum Community Height
Native Species – Species described as being native to the DMP
NAWMP – North American Waterfowl Management Plan
NF – Natural Flooding
NRAL – Natural Resource Analytical Laboratory
Other Waterfowl – All other ducks excluding Northern Pintail
PPR – Prairie Pothole Region
RHR – Relative Height Ratio
RSR – Relative Shoot Ratio
SF – Spring Flooding
VOR – Visual Obstruction Reading

CHAPTER 1

INTRODUCTION

1.1. Conceptual and Philosophical Thoughts

"A problem never exists in isolation; it is surrounded by other problems in space and time: The more of the context of a problem that a scientist can comprehend, the greater are his chances of finding a truly adequate solution" - Ackoff (1962). Moreover, "It is not always possible for the researcher to formulate his problem simply, clearly and completely. He may have only a general, diffuse, even confused notion of the problem. This is the nature of the complexity of scientific research" (Kerlinger 1986). A fundamental principle to scientific inquiry is that, "if a scientist wants to solve a problem, then he must know what the problem is, and try to reduce it to a hypothesis" (Kerlinger 1986). Hypothesis testing is a special case of estimation in which one is interested in determining the possible states that exist, and it is useful in selecting the best decision for problem situations that confront the client or the researcher himself (Ackoff 1962).

The research reported in this thesis was conducted in the above context. It identified problems that arose from the creation of wetlands in the Dry Mixed Grass Prairie (DMP) region of southeastern Alberta, Canada, and provides regional land managers with ecologically adaptive prescriptions for managing such landscapes for sustaining waterfowl and cattle production in the region. Although the results and recommendations contained herein may be most applicable to the study location and the typical land use issues investigated, the overall contribution of the research to scientific knowledge for managing native prairie vegetation and landscapes for both livestock and waterfowl production is substantial.

1.2. Research Rationale

Wetland development projects have been undertaken around the world for various purposes, including the maintenance of wildlife habitats, conservation of wetland-dependent biodiversity, flood mitigation, waste water discharge and treatment, and the provision of water for domestic, agricultural and industrial uses. Within the DMP of southeastern Alberta, Ducks Unlimited Canada (DUC) has created and maintained semi-permanent and permanent wetlands for waterfowl production since 1983. The primary goal of DUC's activity is to enhance prairie breeding habitat for Northern Pintail (*Anas acuta* L.), whose population has experienced nearly 75% decline over the last 50 years (Appendix XVIII) as a result of intensified agriculture and extended drought (Austin and Miller 1995, Chipanshi et al. 2006, Raddatz 2007). These wetland projects have involved agreements with the Eastern Irrigation District (EID) and other Irrigation Districts across the region for access to both land and water for flooding. The EID has ownership rights over the native rangelands flooded to create wetlands in the DMP, and thus manages all livestock grazing dispositions and land uses. The continued support of ranchers for DUC wetland projects depends, in part, on ensuring the proliferation of spikerush (*Eleocharis palustris* L.), a hergage species characteristic of seasonal wetlands preferred by Northern Pintail in the DMP. *E. palustris* is a palatable high quality forage species (Sankowski et al. 1987), and it provides protective cover for waterfowl broods (Jordan et al. 1997).

1.3. Research Problem

Despite the historical success of DUC's wetland program, managing created wetlands is not without challenges. Vegetation within created wetlands appears to have undergone substantial successional change through the development of various plant community types following initial flooding (Fig. 1.1). In well-established wetlands over 20 years old, areas once dominated by *E. palustris* communities are currently dominated by cattail (*Typha latifolia* L.). Although *T. latifolia* communities can provide habitat for some species of waterfowl and wildlife (Gilbert et al. 1996), it may not provide optimum habitats for prairie breeding populations of Northern Pintail and other dabbling ducks, which are known to prefer temporary and seasonal wetlands interspersed within short prairie vegetation (Kaminski and Weller 1992). *T. latifolia* communities may also be less effective in meeting other land uses, including the provision of palatable forage for livestock.

Despite the obvious occurrence of vegetation changes in these wetlands, there is little information on the required hydrologic regimes (either during initial wetland creation or during subsequent flood water management) that can generate and maintain desirable *E. palustris* dominated communities. Where previous flooding has resulted in *T. latifolia* proliferation and compromised the intent of created wetlands by reducing habitat suitability for Pintails, unique management strategies may be needed to control this plant species. Thus, the question of interest to land managers in the DMP, as well as researchers, is whether anthropogenic flooding can be manipulated to develop and maintain a desirable community dominated by *E. palustris* on the landscape (Fig. 1.1).

T. latifolia is a nutrophilic aquatic macrophyte that responds aggressively in growth to nutrient-rich aquatic media, and thus, plays a crucial role in wetland nutrient cycling (Good et al 1978, Newman et al. 1998, LaBaugh and Swanson 1992, Green and Galatowitsch 2001). Both anthropogenic activities (e.g., grazing, mowing, burning, nutrient reduction) and hydrologic manipulations (e.g., the timing, depth and duration of flooding and/or drought stress) can be used to influence the dynamics of wetland biota and associated habitat characteristics (Visser et al. 1999, Bataille and Baldassarre 1993, Poiani and Johnson 1989, Weinhold and Van der Valk 1989, Murkin and Kadlec 1986 a & b). *T. latifolia* proliferation may be curtailed by mowing (Ball 1990, Nelson and Dietz 1966), burning (Ball 1990, Mallik and Wein 1986, Smith and Kadlec 1985), a reduction in wetland nutrient load (Newman et al. 1996), or by hydrologic manipulation such as the introduction of either drought stress or deep flooding (Squires and van der Valk 1992, Ball 1990, Mallik and Wein 1986).

Information from other studies also indicates that factors such as hydrologic regimes, grazing, and water quality, either individually or collectively, influence wetland habitats in terms of the abundance of soil seed bank (Poiani and Johnson 1989, Weinhold and Van der Valk 1989), vegetation composition (Visser et al. 1999, Tanner 1992, Casanova and Brock 2000), and macroinvertebrate distribution and abundance (Bataille and Baldassarre 1993, Murkin and Kadlec 1986 a & b). These in turn, have profound effects on waterfowl distribution and abundance (Murkin and Kadlec 1986a & b). Thus, an understanding of the various factors regulating wetland vegetation and associated wildlife use is imperative for developing improved management systems consistent with maintaining the benefits of created wetlands in the region (Day et al. 1988).

Biologically and economically, hydrologic manipulation, including moisture stress and/or deep flooding, may be a more appropriate method of controlling the spread of *T. latifolia* in the region. This is due to the extensiveness of wetlands, and the ease of floodwater manipulation from irrigation sources. Moreover, practices such as burning are unacceptable within the EID due to the high risk of wildfire associated with the semi-arid climatic conditions of the DMP (Erichsen-Arychuk et al. 2002). Similarly, herbicidal control of *T. latifolia* in the region may be both ecologically and economically prohibitive.

Given the ongoing nature of wetland development in the DMP, there is also a need to better understand the initial hydrologic regimes, including variation in the timing and depth of flooding, necessary to facilitate the growth and establishment of desired plant communities (i.e., *E. palustris*) within newly created wetlands. Furthermore, it is important to understand the combined effects of wetland hydrology, livestock grazing and nutrient accumulation on subsequent plant community development, as well as the associated response of waterfowl (especially Northern Pintail).

1.4. Research Objectives

To understand wetland habitat dynamics and address the above issues of management concern, a four-year field study was initiated within native rangelands of the EID near Brooks, Alberta in August 2002. This investigation was designed to assess the effects of wetland hydrologic regime (with cattle grazing) on vegetation characteristics and breeding waterfowl use of both newly created wetlands and older established ones. The overall goal was to understand vegetation responses (including native and introduced species composition and diversity, herbage productivity and quality) and breeding waterfowl population responses to hydrologic manipulations such as anthropogenic spring and fall flood augmentation and temporary flood cessation. It aimed at examining spatial and temporal vegetation changes under "grazed" and "ungrazed" conditions.

To explore the specific response of *T. latifolia* and *E. palustris* to various hydrologic regimes, a preliminary experiment was conducted under greenhouse conditions during the fall and winter of 2002/2003 and 2003/2004, using potted soil plugs of *T. latifolia* and *E. palustris* with shoots, rhizomes and roots intact (Chapter 3). This experiment was conducted to provide a basic understanding of the morphological and biochemical responses of *T. latifolia* and *E. palustris* to varying periods of soil moisture stress and subsequent reflooding, the results of which are useful in identifying moisture thresholds for replacing *T. latifolia* in favor of *E. palustris*. This study also provides a framework for understanding and interpreting the observed vegetation responses in the field-based study, which were conducted under stochastic environmental conditions.

The associated field study evaluates plant community responses along a catena topo-sequence to spring and fall seasons of flood augmentation during initial wetland development (Fig. 1.1) (Chapter 4). A second component of this study describes community change within older established *T. latifolia*-dominated wetlands subjected to either a change in the seasonality of flooding or short-term flood cessation (Fig. 1.1). Environmental variables with potential effects on plant community succession and changes within the study wetlands are also assessed in Chapter 4. These include the spatial and temporal dynamics of soil moisture and soil available nutrients such as nitrate, ammonium and phosphate.

Herbage productivity and quality responses to the various hydrologic treatments implemented in both field studies are assessed in Chapter 5, along with patterns of cattle use across various topographic positions. This information will assess the potential of created wetlands to contribute to alternative land use activities in the study area.

Breeding waterfowl use of the study wetlands subjected to varied flood seasonality and flood cessation is evaluated in Chapter 6. This was accompanied by an assessment of habitat characteristics involving plant community structural dynamics to help understand the potential effects of hydrologic treatments implemented on wetland habitat suitability for breeding waterfowl.

The results from both the greenhouse and field studies are synthesized to develop a new theoretical state-and-transition model intended to optimize desirable plant community development for both waterfowl use and livestock grazing (Chapter 7). Ultimately, the study results and model are being used to recommend flood regimes necessary to maintain desired plant communities such as *E. palustris* and minimize *T. latifolia* encroachment onto created wetlands. It concludes by providing suggestions for managing the timing and frequency of flood augmentation necessary to sustain waterfowl, especially Northern Pintail production, and maintain abundant high quality forage for cattle use in the DMP region.

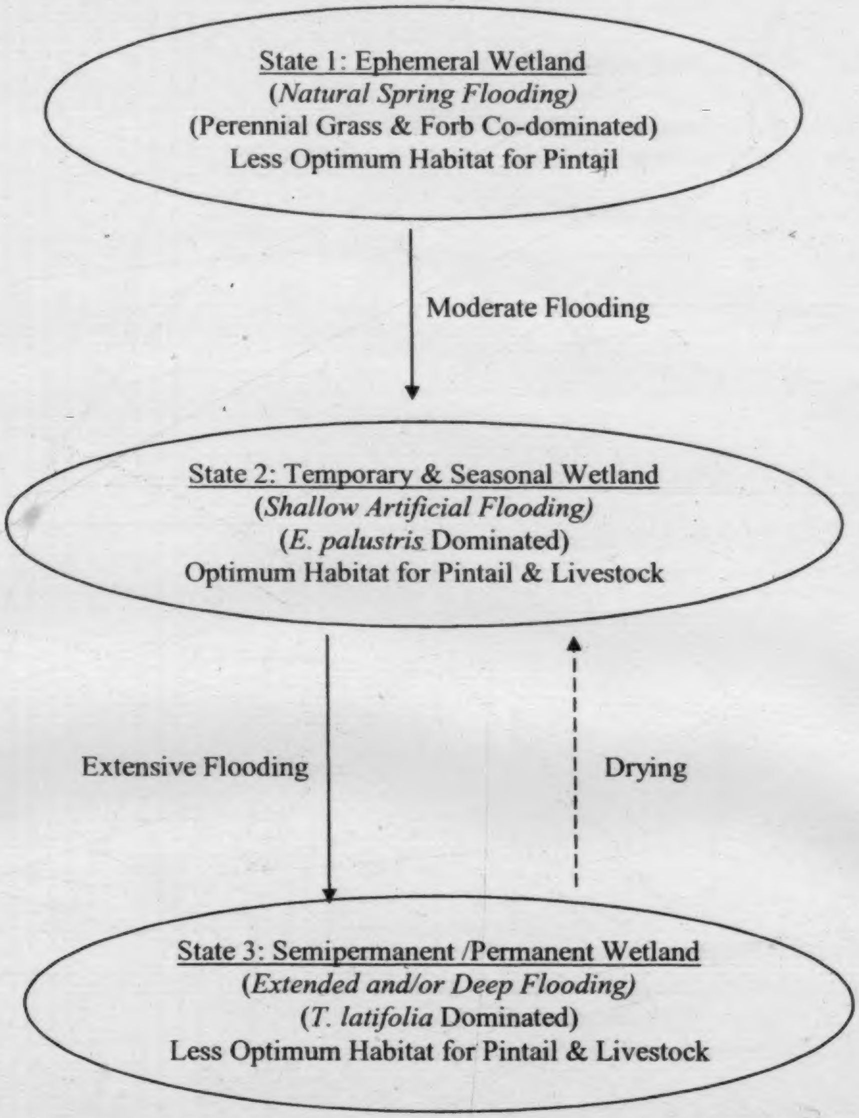
State 1: Ephemeral Wetland
(Natural Spring Flooding)
(Perennial Grass & Forb Co-dominated)
Less Optimum Habitat for Pintail
Moderate Flooding
State 2: Temporary & Seasonal Wetland
(Shallow Artificial Flooding)
(E. palustris Dominated)
Optimum Habitat for Pintail & Livestock
Extensive Flooding
Drying
State 3: Semipermanent /Permanent Wetland
(Extended and/or Deep Flooding)
(T. latifolia Dominated)
Less Optimum Habitat for Pintail & Livestock

Fig. 1.1: Theorized model of vegetation succession following wetland creation in the Dry Mixed Grass Prairie of southeastern Alberta, Canada. State 2 constitutes the desired plant community (DPC) that provides the habitat mosaic optimum for Northern Pintail and rangeland cattle. While moderate and extensive flooding of newly created wetlands may facilitate succession to states 2 and 3, respectively, wetland drying may facilitate community change from state 3 to 2 (the DPC).

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CHAPTER 2

DYNAMICS OF WETLAND ECOSYSTEMS, WATERFOWL HABITATS, AND LIVESTOCK FORAGE - *A LITERATURE REVIEW*

2.1. Wetland Ecosystem Dynamics

2.1.1. Importance of Wetlands

Wetlands provide diverse ecological, economic and recreational values (Mitsch and Gosselink 2000). Hydrologically, wetlands influence the abundance, quality and seasonal patterns of water flow within watersheds. Wetlands in healthy condition can reduce non-point source pollution that might otherwise end up in streams and rivers (Lowrance et al. 1984). They help with aquifer recharge, rebuilding of floodplains and the reduction of stream-bank erosion by storing and slowly releasing water (Elmore and Beschta 1987, Prichard et al. 1993, Prichard et al. 1994). In doing so, they reduce the risk of either excessive flooding or late summer drought (Prichard et al. 1994). Wetland vegetation maintains water quality by removing suspended particles and settling sediments as water moves through them (Prichard et al. 1998).

A large variety of wildlife, including large and small mammals, birds, reptiles, amphibians, fish, and aquatic and terrestrial invertebrates, depend on wetlands for their habitat requirements, either in whole or in part (Thomas et al. 1979, Kauffman and Krueger 1984, Weller 1996). In the Prairie Pothole Region of North America, waterfowl depend heavily on wetlands and the associated uplands as habitats for feeding and nesting (NAWMP 1986, Austin et al. 2001, Emery et al. 2005). During spring and fall migrations, boreal and arctic waterfowl use wetlands in the Prairie Pothole Region as stopover sites for replenishing energy reserves (NAWMP 1986). Other wetland dependent resident and locally migrant wildlife use these areas for feeding, watering, thermal protection, and escape from predators (Weller 1996, Koper and Schmiegelow 2006). Uncontrolled loss of prairie wetlands may pose significant threats to the survival and productivity of large continental waterfowl populations (Leitch and Kaminski 1985, Austin et al. 2001).

2.1.2. Wetland Biogeochemistry and Nutrient Dynamics

Wetlands are described as sources, sinks or transformers of nutrients in the landscape (Mitsch and Gosselink 2000). As sources of nutrients, wetland biota, mostly vegetation and invertebrates, die, decay and decompose to release nutrients locked within plant and animal tissues into the wetland ecosystem. As nutrient sinks, wetlands act as reservoirs for storing nutrients transported into them, either from surface runoff or through ground water movement. As transformers, wetlands convert nutrients and mineral elements from one form to another, either for active uptake and use by other wetland dependent organisms, or loss to the sink pool or atmosphere (Mitsch and Gosselink 2000).

In addition to hydrology, biogeochemical cycling is one of the most important features that characterize wetland ecosystems. This is represented by chemical transformations and transportations within the wetland ecosystem (Mitsch and Gosselink 2000). Chemical transformations involve conversion of the following substances from one form to another under saturated soil conditions: oxygen, nitrogen, iron, manganese, sulfur, carbon and phosphorus. With the exception of gaseous fixation of carbon and nitrogen, these chemicals are transported through wetland hydrologic pathways via precipitation, and surface and ground water movement (Mitsch and Gosselink 2000).

Wetlands soils can be organic or mineral in origin. Organic soils are comprised of dead vegetation at various stages of decomposition that accumulates under anaerobic conditions, and ultimately results in peat formation (Mitsch and Gosselink 2000). The physical properties of peat are dependent on the type of plant material that accumulates, as well as the degree to which organic material is decomposed (Clymo 1983).

Mineral wetland soils on the other hand, are identified through special redoximorphic features formed by the reduction, translocation, and/or oxidation of iron and manganese oxides (Vepraskas 1995). These features include;

i. redox depletions, characterized by low chroma resulting from reduced oxides of iron and manganese,

ii. redox concentrations, characterized by high chroma resulting from accumulations of iron and manganese oxides under oxidized conditions.

Prolonged flooding promotes the occurrence of redox depletions, while redox concentrations are caused by alternating flooding and drawdown cycles typically found in seasonally flooded mineral wetlands. The development of redoximorphic features in mineral wetlands occurs under sustained anaerobic conditions, optimum biological soil temperatures ($\geq 5^0$C), and mediation by microbiological agents (Mitsch and Gosselink 2000).

Mineral wetland soils are also characterized by the presence of an oxidized rhizosphere, a feature that results from the ability of certain wetland plants (e.g., *T. latifolias*) to transport oxygen from above ground stems and leaves to below ground roots, and the eventual diffusion of excess oxygen into the mineral soil matrix immediately surrounding the roots to cause oxidized iron formation (Mitsch and

Gosselink 2000). There is usually a thin layer of oxidized soil in mineral wetlands at the surface of the soil-water interface. Although the deeper layers of wetland soils remain reduced, the thin oxidized layer is critical for chemical transformations and nutrient cycling in the wetland ecosystem (Mitsch and Gosselink 2000). The oxidized surface layer is the zone of high concentrations of oxidized ions, including ferric, manganate, nitrate and sulphate ions, while the reduced ionic forms such as ferrous and manganous salts, ammonia, and sulphides occur in the lower anaerobic layers below the oxidized rhizosphere (Mitsch and Gosselink 2000).

2.1.3. Ecological Processes within Wetland Ecosystems

Wetland ecosystems are dynamic in nature, and ecologically represent the integrated response of plant and animal communities to interactions among biotic and abiotic factors (Hennan 1996). These interactions are often highly complex and lead to difficulty in predicting community responses to management. For example, Kurashov et al. (1996) assessed the factors underlying the association of littoral invertebrate communities with wetland macrophytes and found that several factors, including shoot density, productivity, periphyton characteristics, and heavy metal types and concentrations, were collectively responsible for the distribution and density of invertebrates. Murkin and Kadlec (1986a), in turn, have indicated that macroinvertebrate densities in prairie wetlands significantly influence breeding waterfowl densities.

Elton (1958) indicated that ecosystem productivity is a function of species diversity. In addition, Connell and Slatyer (1977) indicated that maximum species diversity may result from intermediate levels of disturbance within an ecosystem.

Functional interactions among plant and animal communities are fundamental to determining wetland ecosystem dynamics (Connell and Slatyer 1977). Wetland plants and animals occupy various important niches within these ecosystems, and form complex networks of food webs involved in matter and energy transfer (Payne 1986). Typically, trophic relations between invertebrates and waterfowl are of critical importance in the dynamics of wetland ecosystems (Payne 1986).

2.1.4. Models of Vegetation Succession

Community ecologists have theorized models of plant community succession dynamics from various perspectives (Golley 1977). These include the organismic concept of ecosystem dynamics (Clements 1916), the individualistic concept of plant association (Gleason 1962), the initial florists concept proposed by Drury and Nisbet (1973), the relay florists view of Odum (1983), the resource gradient concept of Pickett (1976), the facilitation, tolerance and inhibition models of Connell and Slatyer (1977), the trait-based vital attributes of species (Noble and Slatyer 1980), and the state-and-transition models of Westoby et al. (1989).

State-and-transition models are non-equilibrium models (Ellis and Swift 1988, Allen-Diaz and Bartolome 1998, Stringham et al. 2001, Briske et al. 2003) that provide a simple management-oriented means of classifying the condition of plant communities on the landscape, and to describe the factors that might trigger transitions to alternative states (Baker and Walford 1995, Bestelmeyer et al. 2004). Unlike many other models of community succession, the state-and-transition model of Westoby et al. (1989) acknowledges that successional pathways are complex and do not necessarily converge on a single endpoint described as climax by earlier community ecologists (e.g., Clements 1936). Moreover, ecological sites may be characterized by multiple steady states (Westoby et al. 1989) with thresholds between alternative states (Friedel 1991, Laycock 1991, Briske et al. 2006), and stochastic events influencing the rate and pathway of succession (McPherson and DeStefano 2003, Briske et al. 2006). These stochastic events may originate from climatic, edaphic and anthropogenic influences (Fuhlendorf and Smeins 1997, Fuhlendorf et al. 2001, McPherson and DeStefano 2003, Briske et al. 2006).

Plant ecologists have used state-and-transition models to describe and predict community dynamics in response to disturbance, management and climate change (Briske et al. 2003, Briske et al. 2005, Briske et al. 2006). Such studies have evaluated site-specific dynamics at multiple spatial and temporal scales (Bestelmeyer et al. 2004, Peters et al. 2006). State-and-transition models have been used to evaluate the benefits and potential effects of anthropogenic disturbances such as fire and grazing on upland grasslands (West and Yorks 2002, Boer and Stafford-Smith 2003, Jauffret and Lavorel 2003, Bestelmeyer et al. 2004). The model has also been used to evaluate the effects of climate change on plant community dynamics (Dale and Rauscher 1994, Jauffret and Lavorel 2003, Bestelmeyer et al. 2004). On landscapes where existing plant communities do not support desired outputs such as increased biodiversity and wildlife habitat values, cultural practices (e.g., fire) may be used to redirect community dynamics (Fulbright 1996). Cultural practices, if carefully conceptualized and implemented based on the intermediate disturbance hypothesis principle (Connell and Slatyer 1977), can maximize species richness and diversity (Fulbright 1996). With the exception of studies by Wright and Chambers (2002), who evaluated plant community restoration in response to phreatic depths and burning in riparian zones of the western USA, state-and-transition models have been minimally applied to evaluate plant community dynamics across hydrologic gradients within created wetlands.

2.1.5. Wetland Vegetation Responses to Flooding

Vegetation responses to flooding regimes can be spatially and temporally variable in different regions of the world. According to Clevering and van der Toorn (2000), vegetation succession on the Oostvaardersplassen in The Netherlands during a 7-year study began with domination of mudflat species (*Senecio congestus*) in the first year, only to change to one dominated by *T. latifolia* during the second and third years. Thereafter, common reed (*Phragmites australis*) became the dominant vegetation. Huijser et al. (1995) also used flooding cycles to monitor vegetation succession in wetlands of the Oostvaardersplassen and found that *T. latifolia*s dominated during the first two years after water drawdown. Common reed (*P. australis*) communities succeeded *T. latifolia* within 3 to 6 years of subsequent flooding, and prolonged deep flooding resulted in eventual eradication of vegetation cover (Huijser et al. 1995).

In a study to assess the effects of flooding on Mediterranean wetland plant communities, Mesleard et al. (1999) indicated that flooding favored the dominance of clonal plants and led to a decline in species diversity. Casanova and Brock (2000) used a laboratory study to observe that water regime (depth, duration or frequency of flooding) significantly influenced wetland plant community composition. They indicated that the duration of individual flooding events was important in spatially segregating wetland plant communities. Continuous flooding resulted in low species diversity and productivity, while short but frequent flooding promoted high species diversity and productivity within wetlands. Weller (1978) made similar observations on wetlands in the Prairie Pothole Region of North America and indicated that prolonged maintenance of moderately stable water depths promoted an abundance of rooted aquatic perennials and benthic invertebrates that constituted important food sources for waterfowl. He recommended the introduction of periodic drawdown in prairie wetlands to maintain a diverse stand of emergent vegetation. Weller (1978) further indicated that the maintenance of continuously low water levels for several seasons provided suitable conditions for the growth of *T. latifolia*. Walker and Coupland (1970) assessed wetland vegetation distributions in the prairie and parkland regions of Saskatchewan, Canada, and observed that vegetation type and spatial distribution was greatly influenced by moisture regime, salinity and the intensity of anthropogenic disturbance such as grazing.

2.2. Wetland Plant Ecology, Nutrient Dynamics and Cattail Control

2.2.1. Ecology of Spikerush and Cattail in Wetlands

Water quality influences the type of vegetation found on wetlands. Rejmankova et al. (1995) reported that spikerush (*E. cellulose*) dominated marshy areas with high soil and water conductivities due to the occurrence of gypsum and calcium carbonate. However, nutrient concentrations (nitrogen and phosphorus) were very low in spikerush dominated areas. In contrast, very high nutrient sites were dominated by *T. domingensis* (Rejmankova et al. 1995). Similar studies in the Everglades (Newman et al. 1996, Newman et al. 1998, Turner and Newman 2005, Turner et al. 2006) and Prairie Pothole

Regions (Green and Galatowitsch 2001) indicate that *T. latifolia* responds positively to high nutrient concentrations.

Various species of spikerush occur in different regions of the world. In North American prairies, *E. palustris* is the major spikerush species within seasonal freshwater marshes (Stewart and Kantrud 1971). This species is preferred as cover for waterfowl broods and livestock forage in the Dry Mixed Grass Prairie region of western Canada (Millar 1973, Sankowski et al. 1987). A related species *E. parvula* constitutes an important winter food for waterfowl, especially Gadwall (*Anas strepera*) in southwestern Louisiana, USA (Paulus 1982). In the Canadian prairies, *E. palustris* responds to annual spring moisture recharge by initiating rapid growth to form dense stands (Millar 1973). It is less tolerant of extreme hydrologic conditions, including extended flooding and drought (e.g., Froend and McComb 1994, Sorrell et al. 2002, Santos and Esteves 2002, Busch et al. 2004), which may subject the plant to competitive displacement by other, more productive species under these conditions (Millar 1973, Sorrell et al. 2002).

T. latifolia is a widely distributed species (McNaughton 1966, Morton 1975), although its spatial distribution varies across continents (McNaughton 1966). In North America, the common *T. latifolia* occurs mostly in the west of the continent, while *T. domingensis* Pers. occurs to the south. The narrow-leaved cattail (*T. angustifolia* L.) occurs in isolated areas of the east (Hotchkiss and Dozier 1949, Kantrud *unpubl.*). The hybrid cattail (*T. glauca* Godr.), which is a cross between *T. latifolia* and *T. angustifolia*, is found in isolated places within the Northern Great Plains (Kantrud *unpubl.*). Overall, *T. latifolia* is one of the most common cattail species found on semi-permanent and permanent wetlands in the Prairie Pothole Region of North America (Ralston et al. 2007).

T. latifolia is perennial freshwater plants with extensive and persistent rhizomes, and exhibit aggressive growth within freshwater wetland ecosystems (Grace and Wetzel 1981, Kercher and Zedler. 2004). Structurally and functionally, *T. latifolia*s shape the ecological characteristics of many freshwater wetlands through active biogeochemical cycling, their roles in food webs, and physiological processes (Good et al. 1978). *T. latifolia* rhizomes grow aggressively and produce new shoots annually in response to favorable hydrologic conditions. *T. latifolia* prolifically produces air-borne seeds that easily disperse to colonize newly developed freshwater marshes. By virtue of the plant's affinity for water and extensive rhizome and root system, *T. latifolia* is capable of accelerating wetland xerification under reduced flooding conditions, potentially reducing its own chance of survival (Grace and Wetzel 1981). Notably, *T. latifolia* rhizomes have very high nutritional value and may occupy an important niche in the herbivore and detritus food chains (Furtado and Esteves 1997).

T. latifolia is reported to be highly tolerant of low-redox soils (Pezeshki et al. 1996). This is due to the unique capacity of the plant to create an oxidized rhizosphere around its root system by transporting oxygen from the leaves and stems to the roots (Chabbi et al. 2000).

2.2.2. Nutrient Dynamics in Cattail Shoots and Roots (Rhizomes)

In South Carolina, U.S.A., Sharitz et al. (1984) and Adriano et al. (1984) studied the seasonal growth and dynamics of macronutrients (N, P, K, Ca and Mg) and micronutrients (B, Cu, Fe, Mn and Zn) in the tissues of both the shoots and rhizomes of *T. latifolia* and *T. domingensis* from early to late season in a thermally-graded effluent wetland. They observed that *T. latifolia* growth and nutrient uptake were enhanced by elevated effluent temperatures. Sharitz et al. (1984) noted seasonal declines in the concentrations of macronutrients (N, P, K) in *T. latifolia* rhizomes from early to late season. These declines were rapid during the early growing season and more gradual as the season advanced. This pattern of nutrient uptake may be associated with the plant's initial requirements for those nutrients in order to initiate important physiological processes and metabolism, which seems to follow saturation kinetics. On the other hand, there were different patterns in the seasonal accumulations of Ca and Mg in *T. latifolia* rhizomes. Calcium accumulation increased logistically from the early to late season while Mg levels remained constant. With respect to micronutrients, Adriano et al. (1984) observed that Zn and Fe accumulated in *T. latifolia* rhizomes, while Mn and B accumulated in *T. latifolia* shoots. Copper accumulated in both *T. latifolia* shoots and rhizomes. The concentration of Zn followed similar seasonal trends as those exhibited by N, P and K. Overall, there was more variation in the seasonal dynamics of micronutrients than macronutrients.

In Madrid, Spain, Martin and Fernandez (1992) observed a seasonal decline in N and P concentration in *T. latifolia* shoots. Shoot nutrients were greater during the early phenological growth stage of the plant, implying that there might be active nutrient removal from the wetland at that time. However, as the growing season advanced, *T. latifolia* shoots changed from being a nutrient sink to a nutrient source, with rhizomes taking over the role of nutrient accumulation (Garver et al. 1988). This dynamic has important implications for using *T. latifolia* as bio-filters in purifying eutrophic wetlands, as the plant's ability to take remove phosphates from wetland soils and its potential use as forage by herbivores renders it as an important phytoremediator (Martin and Fernandez 1992, Ciria et al. 2005, Weng et al 2006). *T. latifolia* has been reported to actively take up heavy metals including Se (Azaizah et al. 2006) and Zn, Cd and Pb (Krishnan et al. 1988, Lan et al. 1992), and thus function as bio-filters for these pollutants in purifying wetlands.

2.2.3. Nutrient Dynamics in Cattail-Dominated Wetlands

The nutrophilic property of cattail makes it ecologically important in the wetlands it occupies (Sharitz et al. 1984). It responds significantly to surface water nutrient status (Urban et al. 1993, Rejmankova et al. 1995, Newman et al. 1996, Newman et al. 1998, Green and Galatowitsch 2001, Weng et al. 2006) and has been reported to displace many native wetland plants as a result of nutrient enrichment (Urban et al. 1993, Newman et al. 1996, Rutchey and Vilcheck 1999). In plant mixtures, Newman et al. (1996) reported that *T. latifolia* growth responded positively to both elevated nutrients (by as much as 45%) as well as to increased water depth (by as much as 60%), while wetland species like *Cladium jamaicense* Crantz. and *Eleocharis sp.* did not increase in response to these variables. Furtado and Esteves (1996) indicated that large amounts of nutrients and energy are stored in *T. latifolia* tissues, indicating that the plant is a nutrient reservoir and hence, functionally important by regulating ecosystem nutrient cycling.

In the Delta Marsh of Manitoba, Canada, Kadlec (1986) observed that flooding natural *T. latifolia* dominated marshes to about 1 m above normal did not cause an increase in dissolved or suspended nutrient concentrations in surface water. Instead, concentrations of suspended N, P, and C decreased in surface water while those of major ions such as Ca^{2+}, Mg^{2+}, Na^+, K^+, and Cl^- did not change in response to flooding, despite some temporal and spatial variation. Dissolved forms of N and P increased in interstitial water, possibly as a result of death and decomposition of emergent macrophytes such as *T. latifolia*, and associated wave action and detritus deposition (Kadlec 1986).

T. latifolia is reported to actively take up phosphorus compared to other wetland macrophytes (Lorenzen et al. 2001, Weng et al. 2006) and phosphorus has been reported to be a critical nutrient influencing the specie's expansion in the Everglades of Florida, U.S.A. (Newman et al. 1998, Lorenzen et al. 2001, Miao 2004, Weisner and Miao 2004, Turner et al. 2006). In a seed germination trial, Miao et al. (2001) indicated that *T. latifolia* germination was inhibited under flooded soil conditions but enhanced with saturated soil, while wetland P enrichment resulted in increased seedling growth and asexual (rhizome) propagation.

Newman et al. (1996) found higher P concentration in *T. latifolia* tissues as opposed to those of *Cladium jamaicense*. They indicated that the enhancement of *T. latifolia* by elevated nutrients and increased flooding is associated with a syndrome of *T. latifolia* life history characteristics, which include rapid growth rate, high tissue phosphorus, tall leaves and greater response to contrasting environmental conditions.

2.2.4. Cattail Control

Cattail responds significantly to both surface water nutrient status (Rejmankova et al. 1995, Newman et al. 1996, Newman et al. 1998, Green and Galatowitsch 2001, Weng et al 2006) and hydrologic extremes, including drought stress and depth of flooding (Squires and van der Valk 1992). Saturated hydrologic regimes and phosphorus enrichment are critical factors enhancing *T. latifolia* recruitment (Newman et al. 1998, Lorenzen et al. 2001, Miao et al. 2001, Weng et al. 2006) and attempts to limit the spread of *T. latifolia*s should include reducing surface water nutrient load and imposing extended drought and periodic herbivory (Newman et al. 1996, Pezzolesi et al. 1998). More specifically, limiting phosphorus availability might lead to a reduction in *T. latifolia* abundance (Lorenzen et al. 2001, Miao 2004, Weisner and Miao 2004, Weng et al 2006). This could be achieved through phytoremediation (Doub 2000, Azaizeh et al. 2006, Weng et al. 2006). An alternative approach may be to limit phosphorus inputs from agricultural activities mostly originating from cattle defaecation.

Mowing and burning have been used in the past to control *T. latifolia* (Ball 1990, Smith and Kadlec 1985a). In a case study conducted in southwestern Ontario, Canada, Ball (1990) found that early spring burning or mowing, followed by deep flooding, effectively controlled *T. latifolia*. However, with shallow post treatment flooding, mowed *T. latifolia* was controlled to a greater extent than burned *T. latifolia*. Smith and Kadlec (1985a) made a similar observation in the Great Salt Lake marsh in Utah (USA), and in a related study, found that post-burn grazing reduced the net primary productivity of *T. latifolia* by 48% (Smith and Kadlec 1985b). Nelson and Dietz (1966) also reported that sequential mowing of above ground biomass at a six-week interval effectively controlled *T. latifolia*.

In the Tintamarre Marsh in New Brunswick, Canada, Mallik and Wein (1986) reported that wetland draining and burning produced a significant reduction in *T. latifolia* characteristics, including plant cover, height, stem density and stem basal diameter. The treatments caused an increase in wetland species diversity after three years. Minimal draining resulted in the proliferation of more hygric herbage while mesic species sprouted on completely drained areas (Mallik and Wein 1986).

Concentrated cattle grazing may also be used to control undesirable herbage such as cattail in affected landscapes. For example, De Bruijn and Bork (2006) used a high density rotational cattle grazing to control Canada thistle (*Cirsium arvense*) in the Aspen Parkland region of Canada. Also, cattle have been lured with dehydrated molasses supplement blocks to concentrate grazing in underutilized landscapes in Foothills region of Montana, USA (Bailey and Welling 1999, Bailey et al. 2001).

2.3. Waterfowl Ecology and Management

2.3.1. Breeding Waterfowl Production in the Prairies

The Prairie Pothole Region has colloquially been described as the "duck factory" of North America. Many waterfowl species breed annually in the region (Austin et al. 2001). However, populations of several species of waterfowl have suffered drastic declines in the region over the last few decades (Dickson 1989, Caithamer et al. 1992). Two major factors may account for these declines, including those of anthropogenic and natural origin. The former relates to habitat loss due to wetland draining and agricultural expansion (Boyd 1985, Millar 1989, Nudds and Clark 1993, Podruzny et al. 2002), while natural factors pertain to drought that has affected the prairies since the early 1960s (Nudds 1983, Johnson and Grier 1988, Williams et al. 1999, Chipanshi et al. 2006). The combined effects of these factors have culminated in the loss of prairie wetlands and suitable nesting habitats (Turner et al. 1987, Johnson and Grier 1988) and eventually led to large reductions in Northern Pintail numbers across the region (Podruzny et al. 2002).

In addition, extensive practice of spring tillage on many croplands in the Prairie Pothole Region is a major cause of nest destruction. In particular, crop stubble serve as ecological trap for Northern Pintail, which typically nests stubble, only for them to be destroyed by farm machinery during spring tillage (Devries and Moats *unpubl.*).

Waterfowl management may involve ecological manipulations to change either recruitment or survival rates (Koeln et al. 1996, Emery et al. 2005). Factors controlling these demographic functions include the amount and type of habitat, population density, disease and predation, with waterfowl management mostly consisting of manipulations that preserve, add or modify habitats (Koeln et al. 1996). The most difficult decision confronting the waterfowl biologist is selecting habitat manipulations that, alone or in combination, will have the desired effect on waterfowl productivity. This is because of the many habitat variables involved, as well as the complexity of biological interactions among species of waterfowl and individual habitat requirements (Koeln et al. 1996).

Annual waterfowl recruitment is associated with the reproductive success of individual species. Simulation studies indicate that waterfowl recruitment rates are sensitive to the proportion of adults that attempt to breed (Johnson et al. 1992). In North America, waterfowl within the temperate, subarctic and arctic regions have a narrow window of opportunity to effect annual reproduction against the odds of environmental hardships and uncertainties from year to year. For these waterfowl, it is necessary to breed, nest, brood and fledge young during spring and summer when environmental conditions may be favorable.

Seasonally migrant waterfowl that breed within the temperate and arctic regions of North America rely on photoperiod as the mechanism for providing a stimulus for migration and reproduction (Farner 1964, Immelmann 1971). The "clock" that triggers egg-laying among breeding waterfowl is also related to ambient temperatures during spring, with nest initiation occurring earlier when spring temperatures are relatively warm (Langford and Driver 1979, Krapu and Doty 1979, Fredga and Dow 1983, Greenwood et al. 1995). Ambient temperature also correlates positively with food availability, thus exerting synergistic effects on the timing of nest initiation (Krapu and Reinecke 1992, Krapu 2000). With the exception of Godin and Joyner (1981) and Kaminski and Prince (1981), who reported no discernible relationships, a number of studies have observed positive correlations between invertebrate abundance and breeding dabbler habitat use (e.g., Joyner 1980, Murkin et al. 1982, Murkin and Kadlec 1986, Ball and Nudds 1989, Foote and Hornung 2005). Food availability is related to the frequency and amount of precipitation, as well as fluctuating water levels in wetlands (Braithwaite and Frith 1969). These factors combined provide a reliable indication of the annual foraging opportunities available for several species of waterfowl and hence, opportunities to reproduce during any particular year. Unfavorable conditions within staging and/or breeding areas may cause waterfowl to forgo breeding attempts altogether (Smith 1969, Smith 1971, Krapu et al. 1983, Krapu and Reinecke 1992, Krapu 2000). Nest success is one important factor influencing waterfowl recruitment. Nest fate after a predatory activity has important implications for nest success and ultimate population recruitment (Ackerman et al. 2003). Some waterfowl species such as Mallards (*Anas platyrhynchos* L.) are very sensitive to egg loss from the clutch, and females may decide to abandon the entire clutch under such situations (Ackerman et al. 2003). A female's decision to stay with or abandon the reduced clutch has an important influence on nest success (Ackerman et al. 2003).

2.3.2. Special Case of Northern Pintail Production in the Prairies

The Northern Pintail (*Anas acuta* L.) is a migratory waterfowl species that breed in the Prairie Pothole Regions of southwestern Canada (Austin and Miller 1995). They are among the first migrant waterfowl species to arrive in the region soon after snow-melt in spring. They respond to favorable wetland conditions by rapidly initiating breeding and nesting activities (Austin and Miller 1995, Guyn and Clark 2000). Being an early nesting species, they often encounter light snowfall during egg-laying and incubation (Bellrose 1980). They have short incubation periods (Bellrose 1980) and relatively small clutch sizes (Austin and Miller 1995). Under drought conditions, Northern Pintails may forgo breeding attempts (Krapu and Reinecke 1992, Krapu 2000, Guyn and Clark 2000) as drought adversely affects duckling survival (Guyn and Clark 1999). With the occurrence of drought in the prairies, Northern Pintails tend to migrate further north to the subarctic and arctic regions (Smith 1970, Derksen and Eldridge 1980). The probability of successful nesting by prairie-nesting Pintails that migrate further north in response to regional drought is very limited (Derksen and Eldridge 1980). This is because fat reserves become depleted, and food sources further north may not be sufficient to support reproduction (Calverly and Boag 1977).

Northern Pintails have limited capacity to re-nest during late spring, and this is a critical factor contributing to their population decline in the Canadian Prairies (Austin and Miller 1995, Krapu et al. 2002). Typical nesting landscapes include open /short grasslands interspersed with shallow seasonal wetlands that have emergent vegetation (Stewart and Kantrud 1973, Kaminski and Weller 1992). These habitats were historically abundant in the prairies and held the highest populations of breeding Northern Pintails in

North America (Austin and Miller 1995). Stewart and Kantrud (1973) indicated that in North Dakota, U.S.A., 40% of Northern Pintail pairs were commonly found on seasonal wetlands, 24% on cultivated wetland basins, 19% on semi-permanent wetlands, and very few pairs were on permanent wetlands, streams, and reservoirs or large impoundments.

Northern Pintails typically nest at an average distance of 1 – 2 km away from wetlands (Duncan 1987). This nesting behavior is a probable mechanism for avoiding nest and hen depredation, which tends to be concentrated around wetlands where predators congregate to hunt (Duncan 1987). Breeding pair density is positively correlated with wetland size and the number of seasonal wetlands in spring (Stewart and Kantrud 1974), as well as the degree of interspersion of emergent plant cover and open water within wetlands, with densities being greater in habitats where there is greater interspersion (Kaminski and Prince 1984). Such a habitat mosaic enhances invertebrate production, which is a major diet of breeding hens (Kurashov et al. 1996).

Northern Pintails show breeding site fidelity as long as such habitats continue to be suitable for breeding from year to year (Sowls 1955). Unfortunately, Northern Pintail breeding habitats are under serious threat as a result of the massive conversion of native grasslands into agricultural lands (Miller and Duncan 1999).

2.3.3. Factors Affecting Northern Pintail Production in the Prairies

The reason the Prairie Pothole Region in Canada serves as prime breeding habitat may be related to the foraging ecology of Northern Pintail (Murkin et al. 1982, Murkin and Kadlec 1986). Factors that may influence Northern Pintail recruitment include the availability of food, suitable nesting cover, nest site security from predators, wetland flooding, and the availability of wetlands suitable as habitat for hens with broods (Kaminski and Weller 1992).

Northern Pintails are opportunistic omnivores, feeding primarily on invertebrates and small plant parts (Frederickson and Heitmeyer 1991). On wintering grounds in California, food selection is reported to be highly dependent on availability (Euliss and Harris 1987, Miller 1987). However, on spring and summer breeding grounds in the Canadian Prairies, nesting females select invertebrates over plant-based food sources (Krapu 1974b).

Invertebrate food sources become critical during pre-laying and egg-laying periods: the species commonly eaten include high protein and calcium rich macroinvertebrates such as chironomids, gastropods, crustaceans, and oligochaete worms (Krapu 1974a and b, Krapu and Swanson 1975, Frederickson and Heitmeyer 1991, Kaminski and Weller 1992). Invertebrates, particularly chironomids and gastropods, constitute between 67 and 80% of the diet of Northern Pintail ducklings during the first 40 – 50 days after hatching (Sudgen 1973, Krapu and Swanson 1975). These invertebrates, especially the chironomids, are highly preferred and become abundant soon after snowmelt in the numerous shallow wetlands dispersed across the prairies (Frederickson and Heitmeyer 1991). Chironomids typically occur in shallow wetlands less than 4.5 dm deep, with the greatest abundance in wetlands up to 1.5 dm (Frederickson and Heitmeyer 1991).

Typical plant foods include seeds and small underground tubers during spring and summer. Plant foods include smartweed (*Polygonum sp.*), pondweeds (*Potamogeton sp.*), sedges (*Carex sp.*), bulrush (*Scirpus sp.*), and agricultural grain crops (Frederickson and Heitmeyer 1991). Dependence on low quality plant diets during egg-laying results in lower egg production, fertility and hatchability (Krapu and Swanson 1975).

Quality of nesting habitat is an important factor that may affect Northern Pintail recruitment. Historically, Northern Pintails nested primarily in various types of native and introduced upland grasslands (Keith 1961, Stoudt 1971, Greenwood et al. 1995). Presently, many nests are initiated within croplands, brush, and right-of-ways as a result of historical loss of suitable native upland grassland nesting cover caused by intensified agriculture in the prairies (Greenwood et al. 1995). Klett et al. (1988) assessed the relative use of various cover types by Northern Pintails in the prairies and found the following: planted dense nesting cover (43.5%), hayland (14.2%), right-of-way (9.1%), native grassland (8.5%), wetland (6.8%), cropland (5.4%), idle grassland (2.8%), and other areas (9.7%). They observed that although planted cover was the most preferred nesting habitat, it did not necessarily provide greater nest success. Native grasslands provided the greatest nest success rate, emphasizing an important dichotomy between Northern Pintail habitat selection and the suitability of nesting habitats in facilitating duckling recruitment (Klett et al. 1988). Unlike Gadwall (*Anas strepera* L.) and Mallards (*A. platyrhynchos*) that may nest on islands, Northern Pintails rarely do so, and the creation of artificial nesting islands may be less effective in enhancing Pintail production (Duncan 1987).

Anthropogenic activities such as cultivation, livestock grazing, haying and wetland draining are important habitat factors affecting Northern Pintail breeding habitats and nest success rates (Milonski 1958, Krapu 1977, Kirsch et al. 1978, Barker et al. 1990). The conversion of native grassland to cropland across much of the primary prairie breeding and nesting grounds has caused a significant reduction in the hatching rates of clutches laid early in the nesting season (Krapu et al. 2002, Ignatiuk and Duncan 2001). This is because cropland stubble maintained as fallow is a preferred nesting site, and most nests initiated in such areas occur early in the nesting season, only to be destroyed by farm machinery during agricultural land tilling and crop planting in spring (Higgins 1977, Podruzny et al. 2002).

Livestock grazing affects waterfowl recruitment in the prairies (Barker et al. 1990). Direct grazing effects include destruction to nests and the modification of nesting habitat through plant defoliation and trampling (Boyd 1985). A number of waterfowl nests initiated in haylands are destroyed during haying (Higgins 1977, Kirsch et al. 1978).

Other studies have indicated both eggs and hens depredation as additional factors accounting for declines in waterfowl recruitment (Duebbert and Lokemoen 1980). Northern Pintails are highly vulnerable to predation by red foxes within the Prairie Pothole Region (Sargeant et al. 1984). This is because Pintails are the earliest nesters among dabbling ducks in the region, and initiate nesting during early spring when there is poor upland cover and fewer alternative prey sources for foxes (Sargeant et al. 1984, Austin and Miller 1995). Other notable predators of hens, eggs, and ducklings include Northern Harrier (*Circus cyaneus*) Red-tailed hawk (*Buteo jamaicensis*), Common Raven (*Corvus corax*), American Crow (*Corvus brachyrhynchos*), Black-billed Magpie (*Pica pica*), Gulls (*Larus spp.*), American Badger (*Taxidea taxus*), Raccoon (*Procyon lotor*), Weasel (*Mustela* spp.), Stripped Skunk (*Mephitis mephitis*), Mink (*Mustela vison*) and Franklin's Ground Squirrel (*Spermophilus franklinii*) (Austin and Miller 1995).

2.4. Herbage Dynamics and Livestock Grazing on Riparian Wetlands

Riparian zones in healthy condition provide abundant forage for livestock (Willms 1988, Buckhouse and Elmore 1991, Elmore 1992, Svejcar 1997, Asamoah et al. 2004). Enhanced water accumulation in wetlands may increase riparian vegetation growth relative to uplands (Bork et al. 2001) and maintain more favorable forage quality in late summer (Philips et al. 1999, Asamoah et al. 2003). Topographic lowlands and associated riparian meadows have higher grazing capacities, and cattle congregate on such areas relative to adjacent uplands (Reid and Pickford 1946, Pickford and Reid 1948, Roath and Krueger 1982, Willms 1988, Stuth 1993 Van Ryswyk et al. 1995, Asamoah et al. 2003). In the Aspen Parkland of central Alberta, Canada, riparian meadows provide abundant high quality, season-long foraging opportunities for cattle (Asamoah et al. 2004). The strategic use of productive riparian meadows may be economically beneficial to livestock producers through greater weight gains per unit area relative to other topographic positions (Willms 1988, Asamoah et al. 2003, Asamoah et al. 2004). Furthermore, wetlands associated with riparian areas provide a source of drinking water for livestock, and close proximity to water helps in minimizing livestock energy expenditures associated with movements along steep slopes and over long distances in search of water (Reid and Pickford 1946, Roath and Krueger 1982).

Livestock grazing may significantly affect wetland vegetation depending on its intensity. Studies on the Dune Lakes in Northland (New Zealand) indicated that low to moderate grazing maintained greater species and habitat diversities, with heavy grazing producing detrimental effects on vegetation (Tanner 1992). Light grazing also enhanced structural diversity beneficial to wetland dependent wildlife. Similar results have been found within Mixed Prairie upland grassland, where moderate grazing has led to an increase in species diversity (Bai et al. 2001).

Blanch and Brock (1994) investigated the effects of clipping intensity and frequency, as well as the degree of flooding on shoot production and phytomass of both spikerush (*E. acuta*) and *Myriophyllum variifolium* in New South Wales, and reported that *E. acuta* responded poorly to all levels of treatment. They indicated that *E. acuta* might be less tolerant of both livestock grazing and extensive flooding.

Connors et al. (2000) found that disturbances caused by muskrats, including grazing, burrowing and lodge construction, within tidal marshes along the Hudson River of New York, significantly decreased *T. latifolia* biomass and altered wetland soil nitrogen dynamics. In the Canadian prairies, cattle removed more herbage from riparian areas relative to that of other topographic positions (Willms 1988; Asamoah et al. 2003), although the relative degree of use remained similar. In a study by Mesleard et al. (1999), removal of grazing resulted in dominance of the salt tolerant grass *Aeluropus littoralis*. However, combining grazing with summer flooding resulted in dominance of *T. latifolia*s by the third year of the study.

2.5. Management Initiatives for Breeding Waterfowl in the Canadian Prairies

Waterfowl, especially Northern Pintail production in the prairies, is under serious threat from wetland drainage, intensified agriculture, drought and predation (Miller and Duncan). It has been suggested that waterfowl recruitment can be increased through effective habitat management and predator control (Duebbert and Lokemoen 1980, Kantrud 1986, Klett et al. 1988). Prairie waterfowl managers need to embark on efforts to secure less disturbed remnant landscapes for restoration and development as waterfowl habitats (Miller and Duncan 1999). This effort may help increase nest success rates of Pintail and other waterfowl in the region (Bethke and Nudds 1995).

Land tillage has been identified as a major factor affecting waterfowl recruitment in the Canadian Prairies (Frederickson and Heitmeyer 1991). Careful use of agricultural farm machinery to avoid tillage during critical times in the nesting season, as well as no-till practices have been advocated as a means of preventing waterfowl hen and nest destruction (Miller and Duncan 1999). In regions with habitat characteristics that historically attracted Pintails to settle, landowners are encouraged to promote agricultural practices that minimize spring tillage (e.g., the planting of winter crops), convert less productive croplands to perennial forages and pasture, and protect and restore wetland and upland nesting habitats (Podruzny et al. 2002). Gradual flooding and subsequent natural drying (drawdown) of semi-permanent wetlands in spring and summer may create conditions optimum for the production of chironomids and other macroinvertebrates used as food by waterfowl, especially Northern Pintails (Frederickson and Heitmeyer 1991). Periodic flooding and drawdown cycles with flooding depths at ≤4.5 dm may enhance chironomids and macroinvertebrate production (Frederickson and Heitmeyer 1991).

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CHAPTER 3

MORPHOLOGIC AND BIOCHEMICAL RESPONSES OF CATTAIL AND SPIKERUSH TO SOIL HYDROLOGIC TREATMENTS

3.1. Introduction

Species invasions pose a threat to many native ecosystems around the world (Stilling 2002). Invasive plants have adaptations that enable them to out-compete and displace native vegetation, with both natural and anthropogenic factors aggravating this process (Stilling 2002, Myers and Bazely 2003). For example, a change in soil moisture may enable an invasive plant to expand its range and encroach areas not previously colonized (Millar 1973).

To evaluate plant adaptations to management and invasion potential, plant biomass can be partitioned into below ground (root) and above ground (shoot) components. Variation in proportional biomass allocation may be indicative of plant persistence, as affected by moisture gradient, substrate characteristics, summer temperatures and interspecific differences (Gorham 1974, Kvet and Husak 1978). Moreover, changes in proportional biomass allocation may lead to interspecific community changes (Kvet and Husak 1978). Along with biomass, carbohydrate reserves in roots are important for initiating growth in perennial plants following stresses such as drought (Dhont et al. 2002). Decreased carbohydrate concentration is indicative of plant vigor decline, and consequently, its likelihood of persistence (Dhont et al. 2002).

In the Dry Mixed Grass Prairie of southeastern Alberta, Canada, the creation of permanent wetlands from seasonal wetlands by the conservation agency Ducks Unlimited Canada (DUC) has facilitated *T. latifolia* (*Typha latifolia* L.) invasion and displacement of spikerush (*Eleocharis palustris* L.), a preferred species characteristic of seasonal wetlands in the region (Fig. 3.1) (Stewart and Kantrud 1971). The ubiquitous presence of *T. latifolia* is contrary to the original purpose of creating these wetlands, which was to increase the availability of open wetland brood habitat for declining populations of waterfowl, particularly Northern Pintail (*Anas acuta* L.). *T. latifolia* invasion appears to have reduced the value of the resulting plant communities and habitats for waterfowl (Dave Kay *pers. Comm.*), whose populations were noted to increase significantly alongside *E. palustris* abundance soon after initially creating the wetlands in 1983 (Sankowski et al. 1987). Management of *T. latifolia* presents a unique challenge to DUC, whose objective is to reduce this plant, enhance habitats for waterfowl, and restore a community representative of the original seasonal wetlands dominated by *E. palustris*.

T. latifolia is a clonal freshwater perennial plant native to North America (Bedish 1967, Kantrud 1992). It has high photosynthetic efficiency, particularly with abundant moisture during the growing season, and is capable of spreading over large areas via seed dispersal and rhizome expansion (Bedish 1967, Swanson 1987, Li et al. 2004). It has been observed that non-structural carbohydrate (i.e., starch) utilization in *T. latifolia* is rapid during early season growth, with maximum depletion by mid to late summer (Biesboer, 1984). Under prolonged flooding *T. latifolia* rapidly increases to form monocultures (Grace and Wetzel 1981, Swanson 1992) and in doing so, competitively displaces less aggressive flood-intolerant vegetation, and modifies wetland hydrology and associated ecological functions (Millar 1973, Grace and Wetzel 1981, Swanson 1987, Swanson 1992, LaBaugh and Swanson 1992). While prolonged flooding enhances *T. latifolia* vegetative and structural growth, the opposite may occur under drought conditions (Millar 1973, Li et al. 2004).

Similar to *T. latifolia*, *E. palustris* is a clonal freshwater perennial that occurs in seasonal wetlands in North America (Stewart and Kantrud 1971). This species is preferred as cover for waterfowl broods and livestock forage in the Dry Mixed Grass Prairie region (Millar 1973, Sankowski et al. 1987). *E. palustris* responds to annual spring moisture recharge by initiating rapid growth to form dense stands (Millar 1973). It is less tolerant of hydrologic extremes, including prolonged flooding and drought, which may subject the plant to competitive displacement by other species (Millar 1973, Sorrell et al. 2002).

Previous studies have documented the relationship between wetland moisture regime and morphological characteristics of different *E. palustris* species (e.g., Froend and McComb 1994, Sorrell et al. 2002, Santos and Esteves 2002, Busch et al. 2004). Except for cursory studies conducted by Millar (1973) into moisture effects on vegetation in shallow wetlands of south-central Saskatchewan, as well as biomass assessments conducted by Sankowski et al. (1987) in southeastern Alberta, limited information exists on the specific morphologic responses of *E. palustris* to soil moisture regimes in natural and created prairie wetlands across southern Alberta. More importantly, there is no definitive information available on the moisture regime necessary to sustain *E. palustris* while controlling *T. latifolia*, if possible.

Given that land managers prefer *E. palustris* over *T. latifolia* on created wetlands in the Dry Mixed Grass Prairie, there is a need to identify management strategies that sustain *E. palustris* and control *T. latifolia*. Moreover, hydrologic manipulations are feasible within these areas given the artificial origin of these wetlands. Changes in the plant community from *T. latifolia* to *E. palustris* may be possible through the imposition of anthropogenic moisture stress treatments (i.e., cessation of flooding). Before this is done, however, there was a need to understand the specific responses of *E. palustris* and *T. latifolia* to various soil hydrologic treatments, including imposed levels of moisture stress. The intent was to determine the hydrologic field conditions capable of controlling *T. latifolia*, as well as maintain *E. palustris* in the process. Accordingly, a controlled study was conducted in a greenhouse laboratory to assess the survival and morphologic responses of both *E. palustris* and *T. latifolia*, as well as associated carbohydrate reserves of *T. latifolia*, to varying periods of wetland soil drying. It was hypothesized that exposing *T. latifolia* and *E. palustris* to soil moisture stress would adversely impact the biomass and survival of both above and below ground plant components, as well as root carbohydrate reserves necessary for initiating plant growth. However, as *E. palustris* responds in growth to initial flooding on the prairies (Sankowski et al. 1987), it was anticipated that the plant would recover with subsequent reflooding.

3.2. Materials and Methods

3.2.1. Experimental Design

The greenhouse laboratory facility of the Department of Agricultural, Food and Nutritional Science at the University of Alberta was used to perform this investigation. Two separate but complementary experiments were conducted. The first was done during the fall/winter of 2002/2003 to assess *T. latifolia* and *E. palustris* responses to 4 soil hydrologic treatments. A second experiment was conducted only on *T. latifolia* during the fall/winter of 2003/2004, using one of the former treatments and 3 additional hydrologic treatments to serve as an extension of the first experiment. The second experiment became necessary when results from the former could not identify a clear moisture threshold for controlling *T. latifolia*. All experimental materials, including the flood water and plant materials used in both experiments were obtained from the same wetland basin at the Kitsim Wetlands Project (KWP) site in southeastern Alberta, Canada.

Each experiment was set up as a completely randomized design with at least 16 replicates per treatment. Treatments in the first experiment included continuous flooding (CF) where soil moisture was maintained at a 10 cm flooding depth, soil at field capacity (FC) moisture, and 2 intended drought treatments [soil drying for 4 (DS4) and 6 (DS6a) consecutive weeks, respectively]. Treatments in the second experiment involved both overlap and extension of the two drying treatments from the first experiment, including continuous soil drying for 6, 8, 10 and 12 weeks (DS6b – DS12). Treatments DS6a and DS6b were indicative of 6-week drying in the first and second experiments, respectively, and enabled comparison of a common treatment in the 2 separate experiments. These moisture treatments were chosen systematically to enable a clear-cut identification of the moisture threshold capable of controlling *T. latifolia*.

3.2.2. Experimental Procedure

Soil plugs of young *T. latifolia* (approximately 30 - 50 cm height) and *E. palustris* (approximately 20 - 30 cm height), each with shoots, rhizomes and roots intact, were dug up with a garden spade from an existing lentic wetland basin at the Kitsim Wetland Complex (50°29'60''N; 112°06'04''W) located within the Eastern Irrigation District near Brooks, Alberta, Canada. Each plug was transplanted into a 15 cm perforated greenhouse pot that allows free drainage to occur from the base. The potted plants were immediately placed in a greenhouse environment, either in October 2002 (Experiment 1 – *T. latifolia* and *E. palustris*) or August 2003 (Experiment 2 – *T. latifolia* only). All pots were initially subjected to 4 weeks of continuous flooding within specially constructed basins to uniformly acclimate plants to similar pre-treatment hydrologic conditions (i.e., saturation) (Plate 3.1). Flooding depth during acclimation was maintained at 10 cm above soil level in the experimental pots, similar to the flooding depth on the field at the time sample collection from the lentic wetland system at Kitsim. Water for flooding the basins was obtained from the same wetland where the greenhouse plant materials were obtained to simulate field conditions as closely as possible. Analyzed water samples indicated total Kjeldahl nitrogen (TKN) levels were 4.93 mg l^{-1} and total phosphorus (TP) 0.33 mg l^{-1}. Throughout both greenhouse studies, all experimental materials were maintained at 23°C and approximately 70% relative humidity with a 16 hr daily photoperiod to simulate field conditions in the summer when active plant growth occurs.

At the end of the standardized acclimation period, all pots were drained by siphoning out flood water from the basins (Plate 3.1). The pots were then randomly assigned into groups of 16 replicates and the groups of replicates placed in separate basins for the application of individual moisture treatments. Only the CF condition (control) was achieved by adding water to the assigned treatment basin to maintain a 10 cm flood level similar to the condition at acclimation. The FC condition was maintained by adding water every 3 – 4 days and ensuring free drainage and no moisture connectivity among pots, making them independent of each other. No watering occurred in the DS4 to DS12 treatment basins, and the experimental plants were completely independent of each other. In essence, only in the CF treatment had the likelihood being influenced by inter plant (pot) effect due to connectivity via the flood medium, similar to field condition. The rest of the plant materials within the FC – DS12 treatment basins (non-flooded) were disjoint from each other, and thus eliminated any chances of inter plant effects. The CF, FC and DS4 treatments were maintained for 4 weeks, while the DS6, DS8, DS10 and DS12 treatments were implemented for 6, 8, 10 and 12 weeks, respectively (Plate 3.2).

At the end of each specified treatment period, ranging from 4 to 12 weeks in duration, basins were reflooded to saturated conditions for 4 continuous weeks. Reflooding was intended to evaluate the post-treatment recovery of *T. latifolia* and/or *E. palustris* plants previously subjected to varying periods of soil moisture stress.

Volumetric soil moisture (%) was determined both initially (at the end of acclimation) and bi-weekly during treatment applications from a random sample of three *T. latifolia* and four *E. palustris* pots within each treatment using a Delta-T Devices™ ML2x moisture meter that measured moisture within 10 cm depth of soil. Moisture measurements were not performed on all pots to minimize damage from probing into rhizomes and roots.

3.2.3. Vegetation Measurements

Pre-treatment (i.e., prior to drying) data were collected at the end of the acclimation period on maximum plant height and the initial number of live shoots of either *E. palustris* or *T. latifolia* in each pot. Additionally, leaf counts were made on all living *T. latifolia* shoots. Similar repeat measurements of height, shoots and leaves were made periodically during the actual moisture treatment period, and once again in each pot after the 4-week reflooding period ended. Shoot counts were done for both *T. latifolia* and *E. palustris* two weeks into treatment, at the end of moisture treatment, and at the end of reflooding. *T. latifolia* leaf counts were done one more time at the end of application of moisture treatments.

After 4 weeks of re-flooding, all *T. latifolia* and *E. palustris* pots were physically examined to assess plants for signs of shoot regrowth, including the number of live and dead shoots. Any remaining above ground live *T. latifolia* or *E. palustris* shoot material was subsequently clipped in each pot, oven-dried at 60 °C for 72 hr, and weighed. Additionally, soil was washed off *T. latifolia* roots, and rhizomes examined for evidence of live buds. *T. latifolia* roots were then oven-dried at 60 °C for 72 hr, and weighed to determine root biomass. *E. palustris* root biomass was not assessed because of difficulty in separating soil from fine *E. palustris* roots.

Following reflooding, 5 randomly selected samples of live *T. latifolia* roots were harvested from each treatment and ground through a 0.1 mm Wiley Mill ™ screen for the determination of carbohydrate reserves, including total reducing sugar and starch, at the Ecophysiology Laboratory of the Department of Renewable Resources, University of Alberta. The analytical procedure used was a modified Wienmann Enzymatic Method for removing and analyzing non-structural carbohydrates from plant tissues (Smith 1981). Root carbohydrate analysis was done in all treatments except the 12 week (DS12) drying treatment due to high root mortality and insufficient living plant material for analysis.

3.2.4. Data Analyses

Primary response variables within the two experiments included plant shoot and height data, along with *T. latifolia* shoot leaf counts and rhizome mortality. Ending shoot biomass, and in the case of *T. latifolia*, final root mass and carbohydrate levels, were assessed. All datasets were normally distributed prior to analysis according to a Shapiro-Wilk test ($P > 0.05$).

To facilitate analysis, relative ratios of biological data were calculated. Relative ratios, rather than absolute numbers, were used to eliminate potential confounding effects due to non-uniformity in the size of experimental materials at the start of the experiments (Soundy et al. 2001). Ratios have previously been used successfully as indices for measuring plant growth (Lorenzen et al. 2001, Soundy et al. 2001, Santos and Esteves 2002, Busch et al. 2004).

Dependent variables derived for analysis included the relative ratio of live shoots/ramets (RSRs) for both *T. latifolia* and *E. palustris*, plant relative height ratios (RHRs) for *T. latifolia*, and the live leaf density per *T. latifolia* shoot (LLDs). Additional parameters assessed for *T. latifolia* included root mortality, root carbohydrate reserves, and shoot and root biomass. *E. palustris* was additionally assessed for final shoot biomass. Relative shoot and height ratios were determined using the multi-temporal data sampled at either 2 or 3 of the following times relative to the start of treatment application at the end of acclimation:

i. Two weeks into treatment application,
ii. At the end of treatment application (4-12 weeks after beginning), and
iii. After 4 weeks of post-treatment reflooding.

RSR was determined across all treatments in both the first and second experiments using primary data sampled at all 3 time steps (above). RHR was determined in the first experiment alone, and involved use of the first two sampling times (above). RHR was done only for the CF and FC treatments, as *T. latifolia* shoots under the DS4 and DS6a treatments had undergone considerable dieback, and thus, made the determination of live shoot height difficult, if not impractical. LLD determination was done by counting all live leaves per individual *T. latifolia* shoot at both the start and end of treatment applications in the two experiments.

In this study, increases or decreases in RSR and RHR were indicative of a net change in vegetative growth in response to moisture treatment (i.e., duration of drying). While a positive ratio (i.e., > 0) represented net plant growth, a decrease suggested a decline in plant size and loss of vigor. RSRs and RHRs were determined using the relationship (1) below;

$$(R_t - R_i) / R_i \tag{1}$$

where,

R_t represents the plant parameter in a pot at sampling time t, and

R_i represents the initial plant parameter after acclimation.

The use of relative (ratio) data avoided the need for covariates in the analysis of RSR and RHR. However, other dependent variables such as LLD and final root and shoot biomass required the use of covariates during analysis. Thus, both the initial number of live shoots and plant height were used as covariates (one at a time) to assess the influence of initial plant size on subsequent treatment responses. Initial analysis indicated starting shoot density was not a significant covariate ($P > 0.05$) for LLD or biomass (both shoot and root). However, initial plant height was significant ($P < 0.01$) in the analysis of both biomass (shoot and root) and LLD in experiment 2 (Table 3.1). Hence, initial plant height was retained in the statistical models for the analysis of biomass and LLD data.

There was no difference in volumetric soil moisture at the end of the 6 week drying treatment in the first and second experiments ($P = 0.55$). Preliminary analysis of *T. latifolia* data from each of the two experiments indicated that although they were conducted nearly a year apart, the 6 week drying treatments had a similar impact ($P > 0.05$) on *T. latifolia* RSR and root biomass, suggesting that the acclimation periods implemented led to *T. latifolia* plants in similar condition at the start of the treatment phase of each experiment. However, *T. latifolia* LLD and shoot biomass exhibited significant differences between the 6 week drying treatments of experiments 1 and 2 ($P = 0.05$). The reason for this inconsistency is unknown, but might be due to the 2 month difference (i.e., August vs. October) in the time of year when *T. latifolia* plants were brought in from the field, or differences in growing conditions between years.

Based on these inconsistencies, separate ANOVA analyses were conducted on the *T. latifolia* data from each of the two experiments. Statistical tests examined the effects of moisture treatment, plant species and their interaction, on RSR, RHR, LLD and shoot biomass. Relative ratio data were analyzed with repeated measures using 2 to 3 sampling times (depending on the variable). Additionally, LLD data were analyzed as repeated measures using leaf density data at the start and end of treatment applications. Moisture treatments were tested for their effect on shoot and root biomass, and *T. latifolia* root carbohydrate (total free sugars and starch) concentrations.

Analysis used linear additive models for a nested ANOVA (relative ratios and carbohydrate reserves) or ANCOVA (leaf density and biomass) for completely randomized design experiments (Steele et al. 1997). These analyses were conducted using Proc Mixed in SAS (SAS Institute Inc. 2003), with statistical tests considered significant at $P \leq 0.05$ for all treatment effects. Multiple LSmean comparisons on all significant main effects or interactions were performed using Tukey's test ($P \leq 0.05$).

Given the strong similarity in responses among identical treatments within the two experiments, continuous data on *T. latifolia* rhizome mortality, root and shoot biomass, and carbohydrate concentrations, were regressed against minimum volumetric soil moisture measured at the end of each moisture treatment in both experiments to explore the empirical relationships between these parameters.

3.3. Results

3.3.1. Soil Moisture Dynamics

Prior to the implementation of moisture treatments (i.e., soil drying), flooding during acclimation resulted in similar volumetric soil moisture among *T. latifolia* plants in experiments 1 and 2. Similarly, there was no effect of plant species ($P = 0.80$) nor its interaction with moisture treatment ($P = 0.94$) on volumetric soil moisture in experiment 1, indicating trends in soil moisture decline under *T. latifolia* and *E. palustris* were similar (Fig. 3.2). Sequential volumetric soil moisture values taken during experiment 2, and coincident with the FC and DS4 treatments of experiment 1, did not differ ($P > 0.05$). End of treatment volumetric moisture levels within the individual DS6 treatments of experiments 1 and 2 were similar ($P > 0.05$), suggesting parallel patterns of moisture change between the 2 separate greenhouse experiments (Fig. 3.2). Consequently, moisture data from the 2 experiments were combined in subsequent regression analyses.

As expected, moisture treatment had a significant effect ($P < 0.0001$) on volumetric soil moisture in both experiments 1 and 2. In the first experiment, soil moisture was greatest under the CF treatment and lowest under the DS6 at the end of treatment application (Fig. 3.2). A similar pattern was observed in experiment 2, with the FC and DS12 treatments having the greatest and least moisture at 55.8% and 1.5%, respectively. Notably, the greatest moisture loss occurred during the first 4 weeks of drying in both experiments (Fig. 3.2).

3.3.2. *T. latifolia* Shoot Responses (RHR, LLD, RSR, Biomass)

There was no difference in the relative height ratio (RHR) of *T. latifolia* exposed to the CF and FC treatments ($P = 0.34$) in experiment 1, with an overall average RHR of 0.04 at the end of moisture treatment, suggesting minimal height growth in these treatments. Height data were not collected on the other moisture treatments due to extensive dieback of shoot growth.

Moisture treatment and sampling period both had a significant effect ($P < 0.01$) on *T. latifolia* live leaf density (LLD) in experiments 1 and 2 (Table 3.1). There was a moisture treatment by sampling period interaction on LLD in experiment 1 ($P < 0.0001$), but not in experiment 2 ($P = 0.23$). While LLD values were similar among treatments at the end of acclimation within each experiment ($P > 0.05$) (Fig. 3.3), there were inconsistent temporal reductions in LLD across treatments in experiment 1. Temporal reductions in LLD occurred within all treatments ($P < 0.01$) of experiment 1 except the

FC treatment ($P = 0.57$) (Fig. 3.3). Though statistically significant, the LLD reduction within the CF treatment of experiment 1 was relatively limited (Fig. 3.3). In contrast, the DS4 and DS6a treatments in experiment 1 resulted in an 87.7% reduction in LLD. Reductions in LLD were more consistent across all treatments of experiment 2 (Fig. 3.3). The DS8, DS10 and DS12 moisture treatments of experiment 2 had the greatest effect on *T. latifolia* LLD, as no live leaves remained after treatment application (Fig. 3.3). Between experiments, reductions in LLD from the start to end of treatment associated with the DS6a and DS6b treatments were 83.9% and 66.0%, respectively.

There were significant effects of moisture treatment and sampling period, as well as their interaction, on *T. latifolia* RSR in both experiments 1 and 2 ($P < 0.0001$) (Table 3.1). During the first 2 weeks of treatment, no change occurred in *T. latifolia* RSR across treatments in either experiment ($P > 0.05$) (Fig. 3.4). Similarly, no difference in RSR occurred within the CF, FC, DS4, DS6a and DS6b treatments ($P > 0.05$) by the end of moisture treatment. Significant reductions in RSR at that time were limited to the DS8, DS10 and DS12 treatments of experiment 2 ($P < 0.0001$). With reflooding, increases in RSR occurred within the CF, FC, DS4 and both DS6 treatments, with that of the CF and FC being significantly greater ($P < 0.0001$) than the DS4 and DS6a (Fig. 3.4). Drying for 8 weeks or longer in experiment 2 failed to result in recovery of RSR values even after post-treatment reflooding (Fig. 3.4).

T. latifolia shoot biomass varied across moisture treatments in experiment 1 ($P < 0.0001$) but not in experiment 2 ($P = 0.21$). Mean comparisons indicated that shoot biomass in the CF and FC treatments were similar ($P = 0.84$), as were the DS4 and DS6a treatments ($P = 0.99$): however, both pairs differed significantly from each other ($P <$

0.0001). Overall, the CF and FC treatments resulted in the greatest *T. latifolia* shoot biomass in experiment 1 (Table 3.2). Means of *T. latifolia* shoot biomass in the second experiment were similar for all treatments, with an average value of 7.1 ± 0.3 g pot^{-1}. Final *T. latifolia* shoot biomass in the DS6a and DS6b of experiments 1 and 2 also differed ($P = 0.0008$). Regression of *T. latifolia* shoot biomass against end of treatment soil moisture indicated a strong positive linear relationship ($P < 0.01$) (Fig. 3.5).

3.3.3. *T. latifolia* Root Responses (Mortality, Biomass, Carbohydrate levels)

T. latifolia mortality was affected by moisture treatment ($P < 0.0001$). While no mortality occurred of *T. latifolia* plants subjected to the CF and FC treatments, rhizome mortality increased with extended drying, to upwards of 50% mortality when volumetric soil moisture dropped below 5% (Fig. 3.6).

T. latifolia root biomass was significantly affected by moisture treatment ($P < 0.05$) in both experiments 1 and 2. The CF treatment accounted for the greatest root biomass, followed by the FC treatment in the first experiment (Table 3.2). The DS4 and DS6a treatments resulted in similar root biomass, averaging 8.2 ± 0.9 g pot^{-1}. In the second experiment, the DS6b treatment produced the greatest root biomass, with the DS12 producing the least (Table 3.2). However, root biomass of the DS6a and DS6b treatments were similar ($P = 0.48$). Assessed across all treatments, a strong positive linear relationship ($P < 0.0001$) was observed between volumetric soil moisture and *T. latifolia* root biomass (Fig. 3.5). Notably, *T. latifolia* root biomass appeared more responsive to increases in soil moisture than shoot biomass (Fig. 3.5), particularly at moisture levels over 20%.

Moisture treatment affected both total free sugar and starch concentrations in *T. latifolia* rhizomes of experiment 1 ($P < 0.0001$). Overall, concentrations of sugars and starch at harvest were greatest under the CF and FC conditions and lowest under the DS6 (Table 3.3). In experiment 2, total free sugars, as well as starch concentrations, were similar under the DS8 and DS10 treatments ($P > 0.05$), averaging 20.6 ± 0.9 mg g^{-1} and 7.2 ± 2.1 mg g^{-1}, respectively. Notably, these concentrations were not different ($P > 0.05$) from those in the DS6a treatment of experiment 1. Regressed across all moisture treatments, a strong quadratic relationship was observed between end of treatment volumetric soil moisture and *T. latifolia* root concentrations of both total sugars ($P < 0.0001$) and starch ($P < 0.0001$) (Fig. 3.7). Maximum total sugar and starch values were associated with moisture levels of 57.4 and 83.7%, respectively (Fig. 3.7).

3.3.4. *E. palustris* Shoot Responses (RSR and Biomass)

The presence of a 3-way interaction of moisture treatment, plant species and sampling period in experiment 1 (Table 3.1) suggested that *E. palustris* shoots responded differently than *T. latifolia* to moisture levels throughout this trial. Overall, *E. palustris* RSR values (-0.30 ± 0.02) were generally negative and below that of the *T. latifolia* (0.34 ± 0.03). Similar to the *T. latifolia* responses, no change occurred in *E. palustris* RSR within any moisture treatment ($P > 0.05$) during the first 2 weeks of treatment, a trend that continued throughout the application of CF and FC treatments (Fig. 3.8). In contrast, the DS4 and DS6a treatments resulted in a sharp decline in *E. palustris* RSR values ($P < 0.0001$) late into the drying period when volumetric moisture decreased to 11% and 7%, respectively (Fig. 3.8). Furthermore, these differences in *E. palustris* RSR persisted following post-treatment reflooding ($P < 0.001$) (Fig. 3.8). Compared to the *T. latifolia* RSR data (Fig. 3.4), the *E. palustris* results indicate the latter species is much more prone to experiencing declines in shoots, even with short periods of drying. Despite the marked changes in *E. palustris* shoot density, however, *E. palustris* shoot biomass remained similar across all moisture treatments ($P > 0.05$) (Table 3.2) with an average biomass of 4.8 ± 0.25 g pot^{-1}.

3.4. Discussion

Results of this study indicate *T. latifolia* is relatively tolerant of moisture stress, although it is possible to kill the plant with extended soil drying. A 100% root (rhizome) mortality occurred by the 12th week of soil drying, at which time volumetric soil moisture was only 1.5%. While no mortality occurred for *T. latifolia* plants subjected to continuous flooding and field capacity treatments, root mortality increased with extended drying, with over 50 % mortality when soil moisture declined below 5%.

Soil drying affected *T. latifolia* vigor through effects on leaf density (LLD), height ratios (RHR), shoot ratios (RSR), shoot /root biomass and carbohydrate concentration. LLD dynamics provided a rapid indication of the effects of soil drying on *T. latifolia* vigor, with a functional relationship between soil moisture and leaf abundance on *T. latifolia* ramets. LLD decreased with increasing soil moisture stress, declining sharply with 4 and 6 weeks of soil drying at the end of treatment application. However, no live leaves were associated with *T. latifolia*s in soils dried for 8 weeks or longer at the end of treatment application, at which time volumetric soil moisture was $\leq 5\%$. *T. latifolia* under this moisture condition had reduced vigor and were on the verge of mortality. This moisture level is characteristic of arid environments where *T. latifolia* are not supported (Millar 1973, Kantrud 1992). On the other extreme, *T. latifolia* under flooded and field capacity conditions maintained greater leaf growth, reinforcing earlier observations that *T. latifolia* is persistent in wetlands once established (Grace and Wetzel 1981, Swanson 1992).

T. latifolia relative height ratios (RHRs) were also similar under flooded and field capacity conditions. This observation contrasts that of Li et al. (2004), who found *T. latifolia* height to be greater under continuous flooding than pulse flooding (analogous to flooded and field capacity conditions, respectively, in the present study). Although both investigations were conducted in greenhouse settings, different *T. latifolia* propagules were used in each, and may account for the disparity. Nevertheless, RHR results in the present study suggest that once established *T. latifolia* maintains similar structural growth in wetlands under continuous flooding and field capacity conditions, with either being suitable for its persistence (Millar 1973, Grace and Wetzel 1981).

T. latifolia shoot ratios decreased with increasing moisture stress. However, prompt shoot regrowth following post-treatment reflooding of plants subjected to 4 and 6 weeks soil drying suggested that those periods of declining moisture exerted minimal impact on *T. latifolia* vigor. Volumetric soil moisture values coincident with these soil drying treatments were 11 and 7%, respectively. Prompt *T. latifolia* recovery with subsequent reflooding suggests the roots of this species were capable of surviving at these relatively low moisture levels (Grace and Wetzel 1981). In contrast, greater impacts on *T. latifolia* shoot vigor occurred after 8 weeks of soil drying when soil moisture was ≤5%. Moreover, no shoot recovery occurred following post-treatment reflooding, probably due to greater root mortality originating from the lack of moisture (Li et al. 2004). These results suggest 5% may be the moisture threshold needed to hydrologically control *T. latifolia*. On the other hand, greater increases in *T. latifolia* RSR following reflooding of plants subjected to continuous flooding and field capacity treatments corroborates Li et al. (2004) who indicated that such conditions enhance *T. latifolia* growth.

Trends in *T. latifolia* biomass were similar between shoots and roots, with each responsive to moisture stress as exhibited by reductions in the biomass of each component. Regressions of both *T. latifolia* shoot and root biomass on minimum volumetric soil moisture indicated linear relationships in either case, with the greatest reductions in biomass occurring through very low soil moisture (Fig. 3.5). These results affirm earlier observations by Li et al. (2004) that while flooding enhances shoot and root biomass, the reverse holds true under reduced moisture. Although Li et al. (2004) did not detect any such differences, the present results indicate that *T. latifolia* experienced greater biomass allocation to roots than shoots, particularly under continuous flooding and field capacity conditions. These conform to Dougherty and Hinckley (1981), who indicated that perennials generally allocate greater biomass to roots than shoots. However, comparison of the two revealed that the primary effect of initial moisture stress appeared to be a larger reduction in root biomass compared to the shoot component (e.g., Fig. 3.5). Given the larger root component, proportional shoot and root biomass reductions therefore appeared similar with soil drying. The reason for this is unknown but could be due to more rapid root decomposition compared to the shoot.

Results of the *T. latifolia* root carbohydrate assessment indicate that there were general declines in both free sugars and starch concentrations in *T. latifolia* roots with increasing moisture stress, particularly with 4 weeks drying or longer, suggesting that soil moisture is a critical factor in carbohydrate synthesis or utilization in this species. Two major mechanisms may have roles in *T. latifolia* sugar and starch dynamics. First, moisture-stressed *T. latifolia* may have a reduced ability to synthesize and replenish carbohydrates. Second, stressed *T. latifolia* may hasten carbohydrate utilization in order to maintain survival until favorable moisture returns. In either scenario, there appears to be a strong relationship between root carbohydrate and soil moisture, which affects *T. latifolia* vigor (Dhont et al. 2002), and ultimately plant mortality.

Starch concentrations in *T. latifolia* roots were consistently lower than that of free sugars across treatments in both experiments. This difference suggests that free sugar reserves may be a vital source of energy in *T. latifolia* roots, and hence the plant's survival. Although levels of free sugars were similar, starch concentrations under the CF condition were lower than those growing under natural field conditions (Table 3.3). The lower starch observed under greenhouse conditions may indicate a loss of *T. latifolia* vigor in experimental 'control' plants compared to those in natural field conditions, suggesting that while greenhouse conditions facilitated a controlled experiment of moisture stress, this procedure does not entirely represent responses under field conditions. *T. latifolia* sensitivity to other non-perceived ambient factors alongside soil moisture may be involved in carbohydrate synthesis and dynamics. For example, greenhouse plants may have been restricted due to the experimental pots themselves, or moisture in the field may have been more optimal for *T. latifolia* growth.

Regression of total free sugars and starch on minimum soil moisture indicated quadratic relationships, with the greatest free sugar occurring when volumetric soil moisture was about 50%, near FC rather than CF (Fig. 3.7). Although the reason for this is unknown, it is probable that such moisture provided conditions close to optimum for free sugar synthesis.

Compared to *T. latifolia*, *E. palustris* appeared more susceptible to moisture stress with minimal recovery potential. Negative *E. palustris* RSR values were associated with soils dried for as little as 4 or 6 weeks, where volumetric soil moisture contents were 11% and 7%, respectively. The negative RSR is indicative of a net reduction in vegetative growth compared to the initial post-acclimation (i.e., pre-treatment) shoot numbers, and is a consequence of extended moisture stress. Thus, soil drying at or below 11% adversely affected the vegetative growth in *E. palustris*. It is probable that root mortality ensued at this moisture level with minimal chance for recovery during subsequent reflooding. *E. palustris* under experimental CF and FC conditions failed to exhibit additional shoot growth following reflooding. This observation suggests extended flooding may actually be inhibitory to *E. palustris* growth, and corroborates earlier observations by Millar (1973) that continuous flooding may be detrimental to *E. palustris*. However, it is possible that *E. palustris* reached its peak phenological growth earlier due to implementation of the initial 4-week pre-treatment acclimation period, and experimental plants were therefore simply nearing senescence by the end of treatment application. Under natural field conditions, *E. palustris* would likely recover from seeds in the soil seed band. Regardless, these findings suggest that *E. palustris* is less tolerant of extremes in moisture conditions, particularly low soil moisture, and that these conditions may subject this plant species to competitive displacement by others, including *T. latifolia* (Millar 1973, Sorrell et al. 2002).

E. palustris shoot biomass was less affected than shoot densities by the soil moisture treatments investigated. Santos and Esteves (2002) observed that *E. interstincta* attained relatively greater biomass production in wetlands experiencing water level fluctuations. In contrast, Busch et al. (2004) observed that *E. cellulosa* performed better in productivity under stable flooded conditions, as opposed to when exposed to periodic drawdown. The results of the present study do not parallel any of the fore-mentioned investigations, and might be due to *E. palustris* reaching its peak biomass by the end of acclimation, resulting in similar biomass at the onset of treatment application.

3.5. Conclusions and Management Implications

The present study has established that *T. latifolia* is less susceptible to soil moisture stress than *E. palustris*, which has important implications on the use of anthropogenic flooding to manage these two focal species on created wetlands in the Dry Mixed Grass Prairie of southeastern Alberta, Canada. Results indicate that while extended soil drying can be used to control *T. latifolia* shoots at 7% soil moisture, more than 50% of *T. latifolia* roots remained alive at that level. Continuous soil drying for at least 8 weeks was needed to reach ≤5% soil moisture, in turn leading to significant root mortality. Such low moisture levels caused major reductions in root carbohydrates and reduced the potential for *T. latifolia* recovery. In field situations, the maintenance of moisture close to this level is unlikely to be reached, except under the rarest of extended drought condition in the Dry Mixed Grass Prairie.

Unlike *T. latifolia*, *E. palustris* was more susceptible to short-term soil drying, as exhibited through greater declines in plant size and vigor. Extended soil drying may limit *E. palustris* growth and lend the plant to competitive displacement by other species. However, given that *E. palustris* is commonly found in naturally occurring wet meadows (seasonal wetlands) of the Dry Mixed Grass Prairie, which routinely dry out in late summer, this species must have other adaptations enabling it to tolerate these moisture pulses, e.g., abundance of viable seeds in the soil seed bank. Future research is needed to assess plant propagation from soil seed bank, as well as to elucidate the morpho-physiological mechanisms determining drought tolerance in *T. latifolia* and *E. palustris*.

Table 3.1: Summary of statistical tests on the effects of moisture treatment and plant species on relative shoot ratios (RSR), live leaf density per *T. latifolia* plant (LLD), and final shoot biomass (SB) in the first and second experiments.

Experiment	Response	Factor	DF	F Value	Pr > F
1 *T. latifolia* & *E. palustris*	RSR	Plant Species (S)	1	401.11	**<0.0001**
		Moisture Treatment (M)	3	79.98	**<0.0001**
		Species x Moisture	3	0.63	0.60
		Period of Sampling (P)	2	38.21	**<0.0001**
		Period x Species	2	222.57	**<0.0001**
		Period x Moisture	6	34.61	**<0.0001**
		Period x Species x Moisture	6	15.05	**<0.0001**
	LLD[1]	Moisture	3	29.14	**<0.0001**
		Period	1	296.43	**<0.0001**
		Moisture x Period	3	47.11	**<0.0001**
		Initial Height of Plant (covariate)	1	0.72	0.40
	SB	Species	1	16.62	**<0.0001**
		Moisture	3	24.88	**<0.0001**
		Species x Moisture	3	25.17	**<0.0001**
		Initial Height of Plant (covariate)	1	134.78	**<0.0001**
2 *T. latifolia* only	RSR	Moisture	3	55.08	**<0.0001**
		Period	2	317.2	**<0.0001**
		Moisture x Period	6	72.64	**<0.0001**
	LLD	Moisture	3	5.41	**0.0015**
		Period	1	245.98	**<0.0001**
		Moisture x Period	3	1.44	0.23
		Initial Height of Plant (covariate)	1	6.85	**0.01**
	SB	Moisture	3	1.57	0.21
		Initial Height of Plant (covariate)	1	11.87	**0.001**

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[1] LLD was assessed for *T. latifolia* only.

Table 3.2: Mean (± S.E.) shoot and root biomass of *T. latifolia* and *E. palustris* after moisture treatment and 4 weeks of subsequent reflooding in each experiment.

Experiment	Moisture Treatment	*T. latifolia*		*E. palustris*
		Shoot (g /pot)	Root (g /pot)	Shoot (g /pot)
1	Continued Flooding	12.3 ± 0.7a[1]	21.2 ± 2.0a[1]	4.5 ± 0.7
	Field Capacity	11.2 ± 0.7a	16.0 ± 1.9a	5.4 ± 0.7
	Drying Stress for 4 weeks	3.9 ± 0.6b	7.3 ± 2.1b	5.0 ± 0.8
	Drying Stress for 6 weeks	4.3 ± 0.7b	9.1 ± 2.3b	4.3 ± 0.8
2	Drying Stress for 6 weeks	7.9 ± 0.5	7.8 ± 0.7a	-
	Drying Stress for 8 weeks	7.1 ± 0.6	5.9 ± 0.8ab	-
	Drying Stress for 10 weeks	6.6 ± 0.5	5.0 ± 0.7ab	-
	Drying Stress for 12 weeks	6.6 ± 0.5	4.8 ± 0.8b	-

[1] Within an experiment and column, treatment means with different lowercase letters differ significantly ($P < 0.05$).

Table 3.3: Mean (± S.E.) total free sugar and starch content in *T. latifolia* rhizomes after moisture treatment and 4 weeks of subsequent reflooding in each experiment.

Experiment	Moisture Treatment	Total Free Sugar ($mg\ g^{-1}$)	Total Starch ($mg\ g^{-1}$)
1	Continued Flooding	152.5 ab[1]	62.0 a[1]
	Field Capacity	198.1 a	59.7 a
	Drying Stress for 4 weeks	85.2 bc	14.1 b
	Drying Stress for 6 weeks	29.8 c	4.1 b
	S.E. diff.	*18.7*	*11.0*
	F-test, Moisture Treatment	$P < 0.0001$	$P = 0.0007$
2	Drying Stress for 8 weeks	21.5	9.3
	Drying Stress for 10 weeks	19.8	5.0
	Drying Stress for 12 weeks[2]	-	-
	S.E. diff.	*4.1*	*3.1*
	F-test, Moisture Treatment	$P = 0.68$	$P = 0.20$
Check	Field Sample[3]	145.5 ± 24.6	114.6 ± 22.6

[1] Within a column and experiment, treatment means with different lowercase letters differ significantly ($P < 0.05$).

[2] The 12 week treatment resulted in insufficient rhizome biomass for analysis.

[3] Field rhizome samples used as a check were obtained at the time of sampling *T. latifolia* plugs for the second experiment in mid August of 2003.

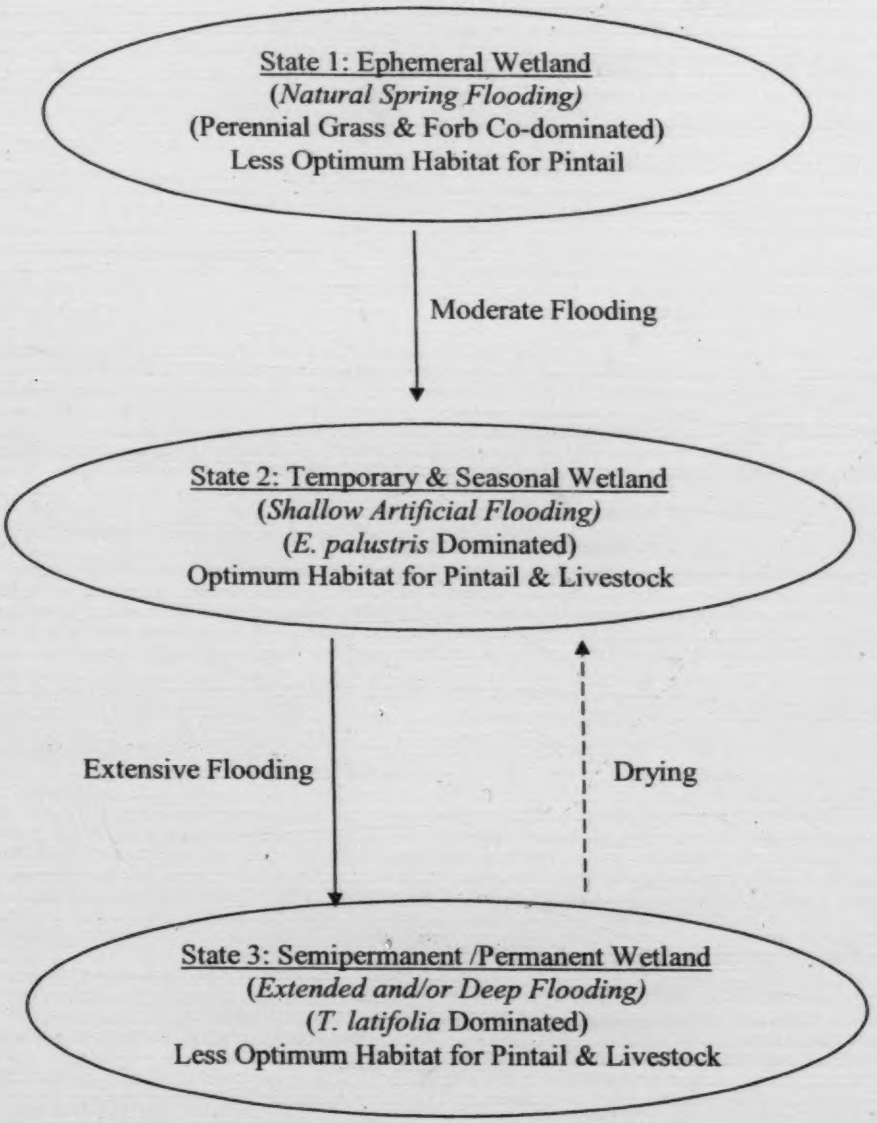
State 1: Ephemeral Wetland
(Natural Spring Flooding)
(Perennial Grass & Forb Co-dominated)
Less Optimum Habitat for Pintail
Moderate Flooding
State 2: Temporary & Seasonal Wetland
(Shallow Artificial Flooding)
(E. palustris Dominated)
Optimum Habitat for Pintail & Livestock
Extensive Flooding
Drying
State 3: Semipermanent /Permanent Wetland
(Extended and/or Deep Flooding)
(T. latifolia Dominated)
Less Optimum Habitat for Pintail & Livestock

Fig. 3.1: Theorized model of vegetation succession following wetland creation in the Dry Mixed Grass Prairie of southeastern Alberta, Canada. State 2 constitutes the desired plant community (DPC) that provides the habitat mosaic optimum for Northern Pintail and rangeland cattle. While moderate and extensive flooding of newly created wetlands may facilitate succession to states 2 and 3, respectively, wetland drying may facilitate community change from state 3 to 2 (the DPC).

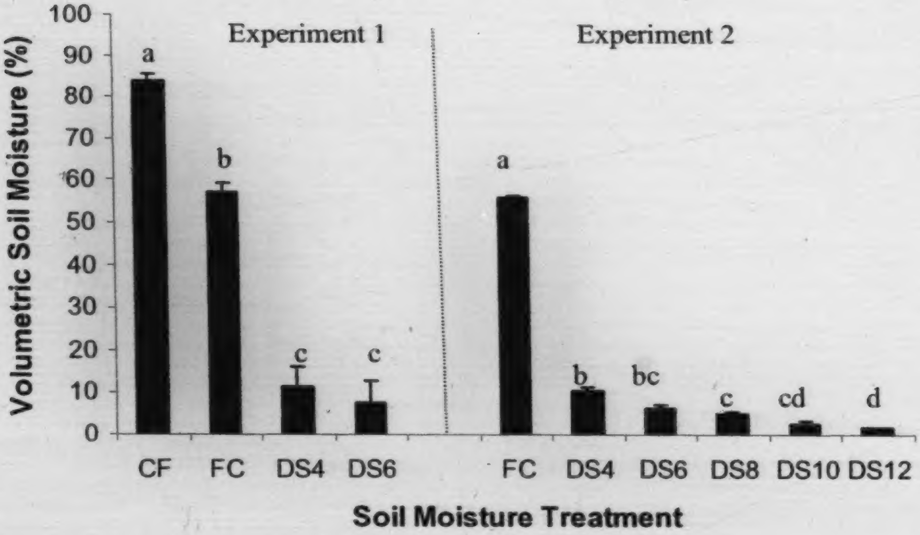

Fig. 3.2: Mean (± S.E) volumetric soil moisture sampled at individual treatment periods in each of the first and second experiments. CF, FC, and DS stand for continued flooding, field capacity and drying stress (with associated number of weeks drying), respectively. Within an experiment, treatment means with different lowercase letters differ significantly ($P < 0.05$). Individual comparison of the FC, DS4 and DS6 treatments between experiments 1 and 2 indicate no differences exist ($P > 0.05$).

√

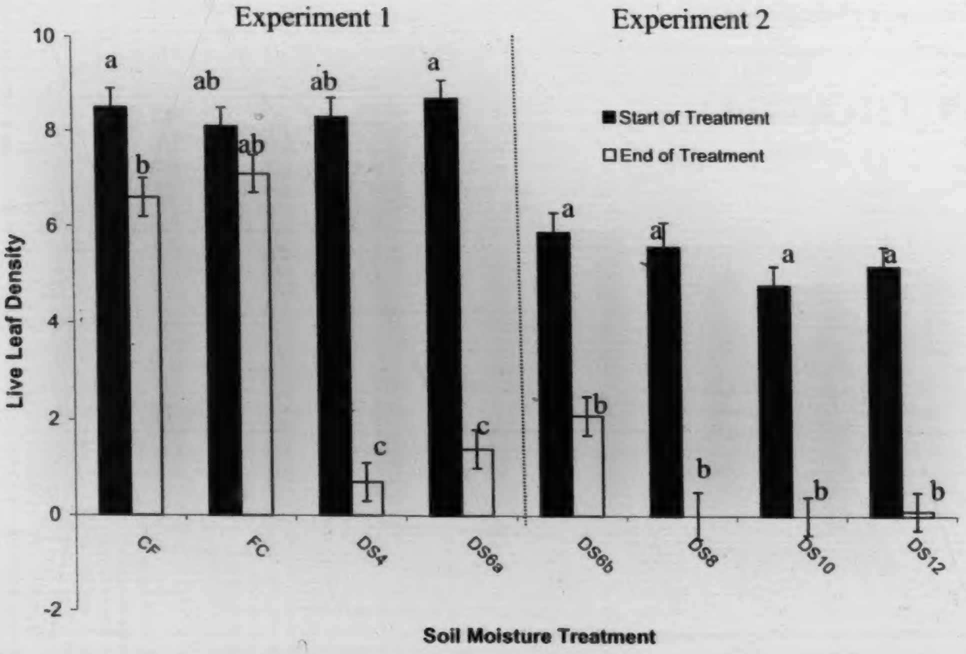

Fig. 3.3: Effects of various moisture treatments on relative live leaf density (LLD) per *T. latifolia* shoot sampled at each of 2 times, including the start of treatment application and again at the end of treatment. CF, FC and DS stand for continued flooding, field capacity and drying stress (number of weeks of associated drying), respectively. Within an experiment, treatment means with different lowercase letters differ significantly ($P < 0.05$).

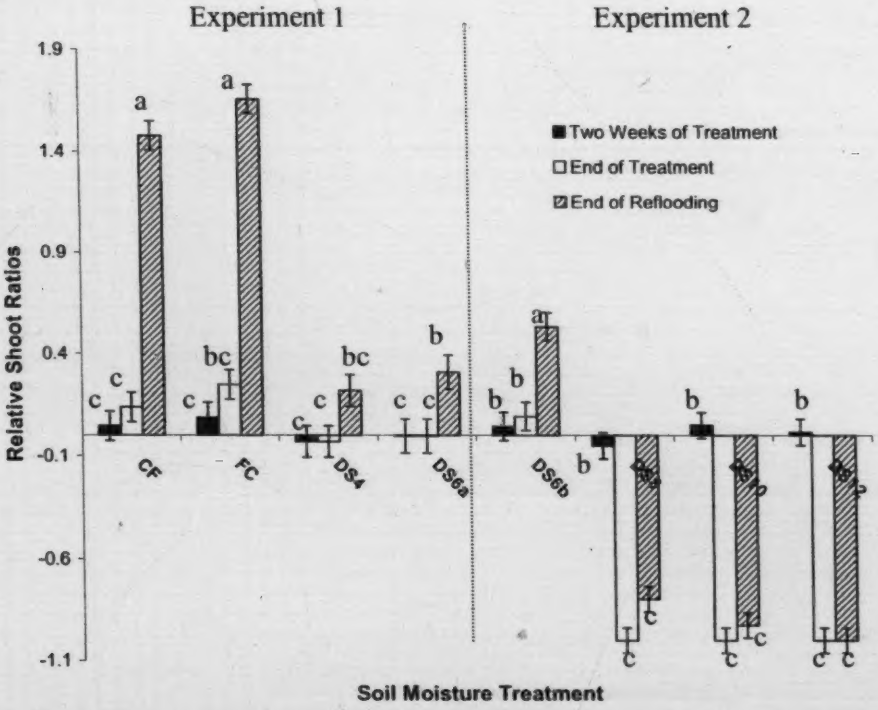

Fig. 3:4: Effect of various moisture treatments on relative shoot ratios (RSR) of *T. latifolia* sampled at each of 3 times, including two weeks into treatment application, at the end of treatment application, and at the end of reflooding. CF, FC and DS stand for continued flooding, field capacity and drying stress (including number of weeks of associated drying), respectively. Within an experiment, treatment means with different lowercase letters differ significantly ($P < 0.05$). Means of the DS6a and DS6b treatments at each of the first 2 sampling times do not differ between experiments 1 and 2 ($P > 0.05$). Means of the DS6a and DS6b treatments at reflooding differ ($P < 0.05$).

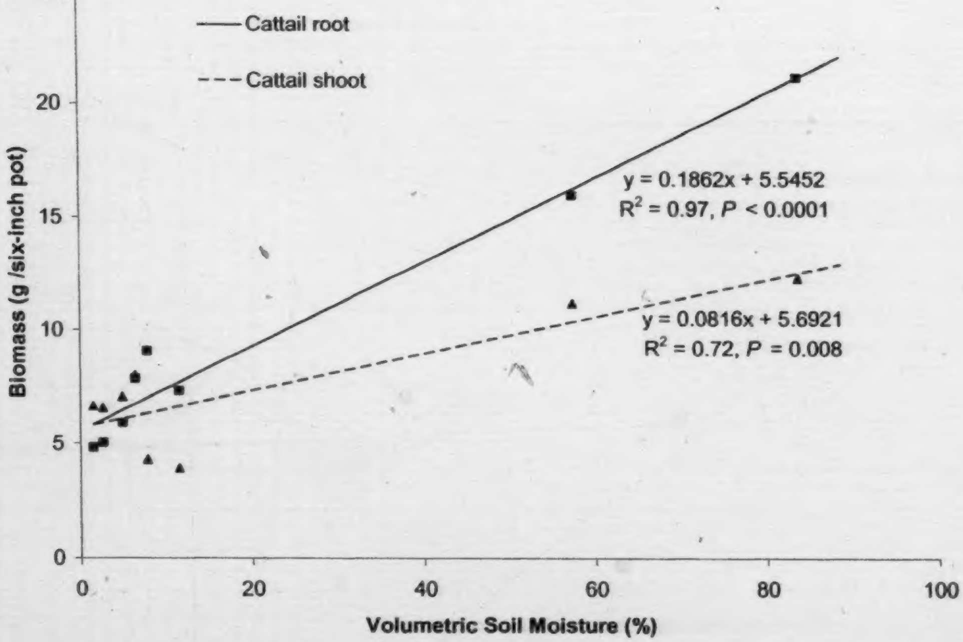

Fig. 3.5: Relationship of final *T. latifolia* shoot and root biomass to end-of-treatment volumetric soil moisture assessed across the 2 experiments.

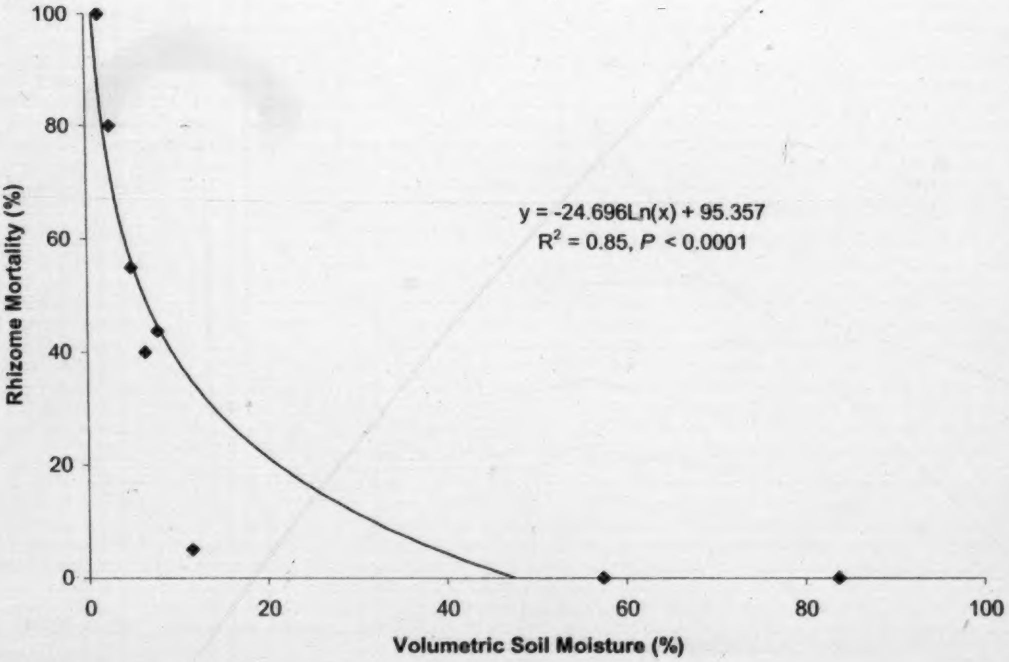

Fig. 3.6: Relationship of *T. latifolia* rhizome mortality to end-of-treatment volumetric soil moisture levels obtained from the 2 experiments.

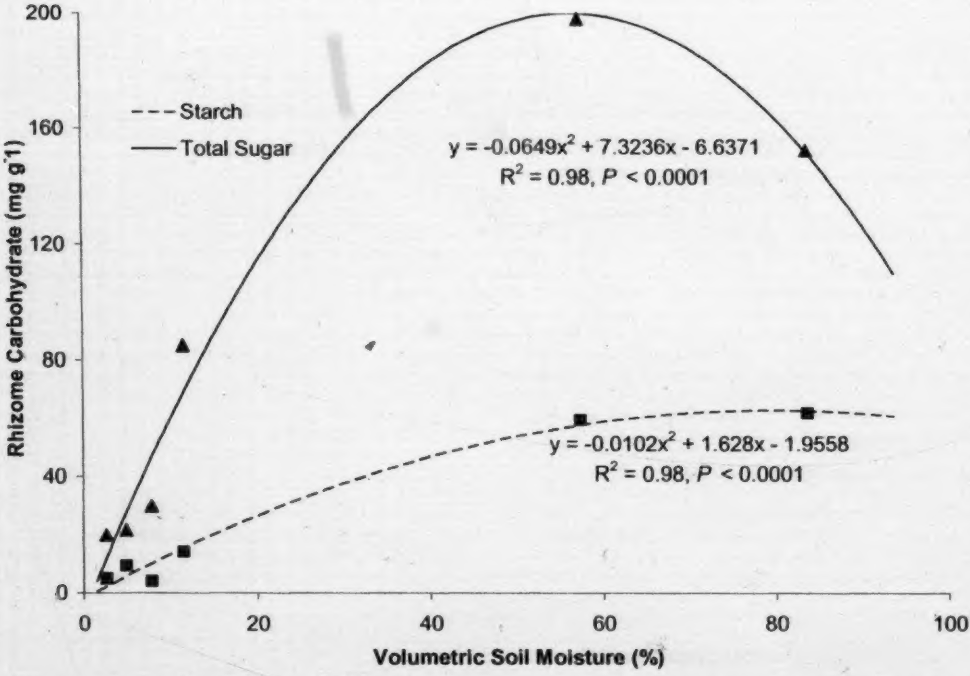

Fig. 3.7: Relationship of total *T. latifolia* rhizome carbohydrates (free sugar and starch) to end-of-treatment volumetric soil moisture assessed across the 2 experiments.

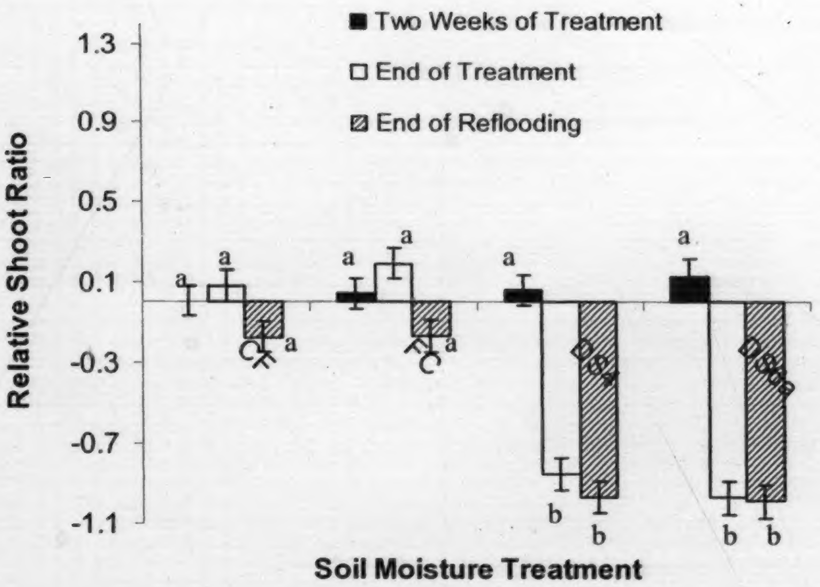

Fig. 3.8: Effects of various moisture treatments on the relative shoot ratio (RSR) of *E. palustris* sampled at 3 different times, including two weeks into treatment application, at the end of treatment, and again at the end of reflooding. CF, FC and DS stand for continued flooding, field capacity and drying stress (number of weeks of associated drying), respectively. Across all means, those with different lower case letters differ significantly ($P < 0.05$).

Plate 3.1: *T. latifolia* plugs at pre-acclimation (top) and post-acclimation (bottom) just prior to the implementation of soil drying treatments in the greenhouse.

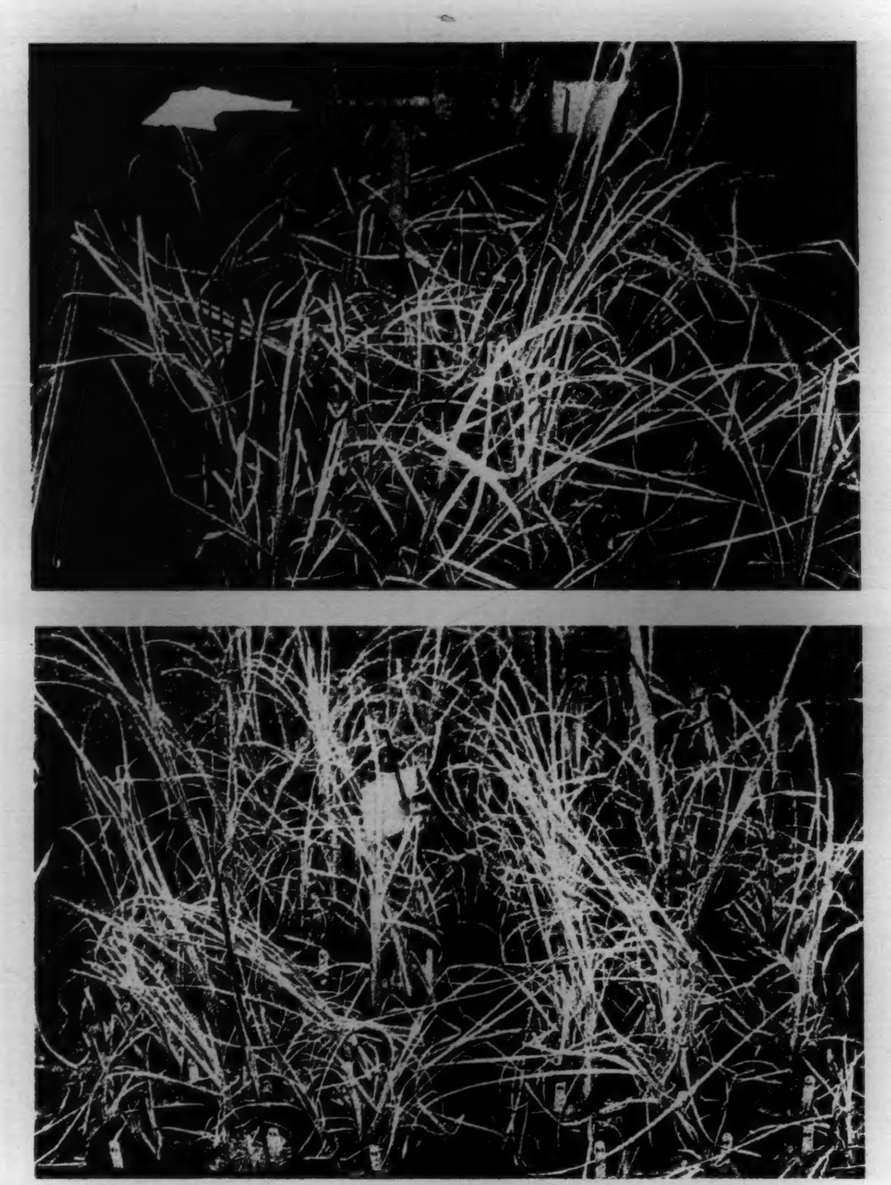

Plate 3.2: Condition of *T. latifolia* plants after 6 weeks (top) and 12 weeks (bottom) of soil drying in the greenhouse. Reflooding was subsequently implemented to assess recovery following each soil drying treatment.

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CHAPTER 4

PLANT COMMUNITY DYNAMICS UNDER HYDROLOGIC GRADIENTS WITHIN CREATED WETLANDS OF THE DRY MIXED GRASS PRAIRIE

4.1. Introduction

Plant ecologists in recent times have used state-and-transition models to describe and predict community dynamics in response to disturbance, management and climate change (Briske et al. 2003, Briske et al. 2005, Briske et al. 2006). Many of these studies have evaluated site-specific vegetation dynamics at various spatial and temporal scales (Bestelmeyer et al. 2004, Peters et al. 2006).

State-and-transition models are non-equilibrium models (Ellis and Swift 1988, Allen-Diaz and Bartolome 1998, Stringham et al. 2001, Briske et al. 2003) that help provide simple management-oriented means of classifying the condition of plant communities across the landscape, and to describe factors that may trigger transitions to alternative states (Baker and Walford 1995, Bestelmeyer et al. 2004). These models acknowledge that community succession is complex and does not necessarily converge on a single endpoint described as climax by previous ecologists (Westoby et al. 1989).

Non-divergent succession within ecological sites is characterized by multiple steady states (Westoby et al. 1989) with thresholds between alternative states (Friedel 1991, Laycock 1991, Briske et al. 2006), and stochastic events influencing the rate and pathway of succession (McPherson and DeStefano 2003, Briske et al. 2006). Stochastic events may originate from climatic, edaphic, natural and anthropogenic influences, and are critical in threshold development (Fuhlendorf and Smeins 1997, Fuhlendorf et al. 2001, McPherson and DeStefano 2003, Briske et al. 2006).

The concept of ecological thresholds has become critically important in the state-and-transition framework as a means of differentiating among various stable states in plant community succession (Friedel 1991, Briske et al. 2006). Using manipulative treatments, ecological thresholds can be managed to prevent the occurrence of undesirable states during succession (Bestelmeyer et al. 2003, Briske et al. 2006). Alternatively, on landscapes where existing plant communities do not support desired outputs such as increased biodiversity and wildlife habitat values, management practices (e.g., fire) may be used to redirect community dynamics and maximize species richness and diversity (Fulbright 1996).

State-and-transition models have been used to evaluate the effects of anthropogenic disturbances such as fire and grazing on upland grasslands (West and Yorks 2002, Boer and Stafford-Smith 2003, Jauffret and Lavorel 2003, Bestelmeyer et al. 2004), or the effects of climate change on plant community dynamics (Dale and Rauscher 1994, Jauffret and Lavorel 2003, Bestelmeyer et al. 2004). With the exception of studies by Wright and Chambers (2002) and Stringham et al. (2001), who evaluated plant community responses to soil moisture and phreatic depths in riparian zones of the western USA, state-and-transition models have been minimally applied to evaluate plant community dynamics associated with hydrologic gradients of created wetlands.

In the early 1980s, Ducks Unlimited Canada (DUC), a private non-profit conservation organization in Canada, under agreements with irrigation administrations and landowners, created semi-permanent and permanent wetlands for waterfowl in the Dry Mixed Grass Prairie (DMP) region of southeastern Alberta, Canada. The original intent of the project was to arrest the decline in breeding populations of Northern Pintail

(*Anas acuta* L.) (Sankowski et al. 1987), which has been associated with intensified agricultural operations and accelerated loss of spring wetlands through drought and wetland draining in the region (Austin and Miller 1995). The DMP is a semi-arid grassland ecosystem characterized by low and erratic precipitation, high summer temperatures, and low primary production (Strong 1992, Adams et al. 2005; Willms and Jefferson 1993).

Research has shown that secondary succession originates with the introduction of a perturbation into a natural ecosystem (Milchunas et al. 1990, Vavra et al. 1994, Mitsch and Gosselink 2000). Anthropogenic activity such as flood augmentation (Wilcox and Thurow 2006) or grazing (Milchunas et al. 1990) is a perturbation that may ultimately modify native ecosystems to the point of facilitating the invasion of non-native plants. Created wetlands in the DMP were established with the use of artificial flooding to augment the moisture level in naturally occurring meadows, originally dominated by native hydric grasses and forbs. Extended flooding results in anoxic conditions in wetland soil, and consequently has critical implications on soil nutrient dynamics (Mitsch and Gosselink 2000). All these factors combined may cause ecological thresholds to be surpassed and lead to another steady state (Briske et al. 2006).

Within three years of initial establishment of created wetlands in the DMP, there was more than a 3-fold increase in spikerush (*Eleocharis palustris* L.) production, a high quality forage species characteristic of seasonal wetlands preferred by Northern Pintails in the DMP, and it contributed locally to cattle foraging (Sankowski et al. 1987). Continued flooding in subsequent years caused cattail (*Typha latifolia* L.) to invade and largely displace *E. palustris* from established wetlands. The apparent shift from *E.*

palustris-dominated communities to *T. latifolia* near-monocultures under extended flooding can be theorized as an initial change in community succession to a state beyond the ecological threshold necessary to maintain *E. palustris* communities (Fig. 4.1) (Friedel 1991, Briske et al. 2006). Moreover, given the highly competitive nature of *T. latifolia* once established (Grace and Wetzel 1981, Swanson 1992) and the observation that the transition from *T. latifolia* back to *E. palustris* appears difficult to achieve due to the greater drought tolerance of *T. latifolia* compared to *E. palustris* (Chapter 3), these patterns suggest non-linear vegetation dynamics may be occurring. Where extended flooding has resulted in *T. latifolia* invasion and there is an interest in restoring more open wetland with low structured plant communities such as *E. palustris*, specific information is needed on the strategies capable of achieving *T. latifolia* control, or reduce its dominance.

E. palustris is a clonal freshwater perennial plant that occurs on seasonal wetlands in North America (Stewart and Kantrud 1971). This species is preferred as cover for waterfowl broods and livestock forage in the DMP region (Millar 1973, Sankowski et al. 1987). *E. palustris* responds to annual spring moisture recharge by initiating rapid growth to form dense stands (Millar 1973). It has limited resilience and is intolerant of extreme hydrologic conditions, including extended flooding and drought (e.g., Froend and McComb 1994, Sorrell et al. 2002, Santos and Esteves 2002, Busch et al. 2004, Chapter 3), which may subject the plant to competitive displacement by other, more competitive species under these conditions (Millar 1973, Sorrell et al. 2002). *E. palustris* normally occurs in less eutrophic systems (Rejmankova et al. 1995) and may be limited by the availability of nitrogen (Sorrell et al. 2002). Under eutrophic conditions, *E. palustris* may be out-competed with increasing phosphorus concentration (Sorrell et al. 2002).

T. latifolia is a clonal freshwater perennial plant native to North America (Bedish 1967) occurring on semi-permanent and permanent marshes in the region (Kantrud 1992). It has high photosynthetic efficiency, particularly with abundant moisture during the growing season, and is capable of spreading over large areas via seed dispersal and rhizome expansion (Bedish 1967, Swanson 1987, Li et al. 2004). Non-structural carbohydrate (free sugar and starch) concentration in roots is critical for plant persistence (Linde et al. 1976, Dhont et al. 2002, Chapter 3). Starch concentration in *T. latifolia* roots is related to soil moisture, peaking at saturated moisture conditions (Chapter 3). Starch utilization is rapid during early season growth, with maximum depletion by mid to late summer (Linde et al. 1976, Biesboer, 1984).

T. latifolia is a nutrophile (adapted to high nutrient levels), and this property makes the plant ecologically important in wetlands (Sharitz et al. 1984). It responds positively in growth to elevated nutrients, particularly phosphorus (Urban et al. 1993, Rejmankova et al. 1995, Newman et al. 1996, Newman et al. 1998, Green and Galatowitsch 2001, Weng et al. 2006), and has been reported to displace native plants as a result of wetland nutrient enrichment (Urban et al. 1993, Newman et al. 1996, Angeloni et al. 2006). Under prolonged flooding *T. latifolia* rapidly increases to form monocultures (Grace and Wetzel 1981, Swanson 1992) and in doing so, competitively displaces less aggressive flood-intolerant vegetation, and modifies wetland hydrology and associated ecological functions (Millar 1973, Grace and Wetzel 1981, Swanson 1987, Swanson 1992, LaBaugh and Swanson 1992, Angeloni et al. 2006). While extended flooding enhances *T. latifolia* vegetative and structural growth, the opposite may occur under drought conditions (Millar 1973, Li et al. 2004). Anecdotal field evidence suggests that livestock foraging on *T. latifolia* may reduce its vigor in the long-term (Appendices XXVI and XXVII).

Various researchers have documented active *T. latifolia* control methods, including wetland nutrient reduction (Newman et al. 1996, Pezzolesi et al. 1998, Lorenzen et al. 2001, Miao et al. 2001, Miao 2004, Weisner and Miao 2004), mowing and burning (Nelson and Dietz 1966, Smith and Kadlec 1985a & b, Ball 1990), herbicide application (Comes and Kelly 1989, Thorsness et al. 1992, Homan et al. 2004), and combined wetland hydrologic manipulation and burning (Mallik and Wein 1986). Many of these control methods may be cost prohibitive or less effective on large-scale wetlands such as those created in the DMP region. Herbicide application is typically prohibited in wetlands, and burning is banned in most regions of the DMP because of economic, social and ecologic considerations. Thus, alternate methods to control *T. latifolia* are required.

The ability to readily manipulate wetland hydrology within created wetlands makes this approach feasible as a management tool to modify wetland communities (Armentano et al. 2006) (Fig. 4.1). Hydrologic manipulation has the advantage of being ecologically friendly and less expensive to implement. Similar to the situation in established wetlands already containing *T. latifolia*, there is limited information on the initial flood regime necessary to maintain *E. palustris* and minimize *T. latifolia* expansion within newly created wetlands of the DMP (Fig. 4.1).

Based on the theoretical state-and-transition model proposed here (Fig. 4.1), an important question of interest in the current study is whether anthropogenically induced wetland community change (e.g., from *E. palustris* to *T. latifolia*) is reversible with the removal of artificial flooding, and if so, under what circumstances (i.e., duration of flood removal or wetland 'drying'). Moreover, information is needed on the rate of plant community and edaphic change occurring across the landscape, as different flooding depths may differentially affect plant species composition, as well as soil physical and biochemical characteristics (Wright and Chambers 2002, Henszey et al. 2004, Laiho et al. 2004). Lastly, it is poorly understood whether artificial flooding during either spring or fall results in different plant community dynamics, both within new and well-established created wetlands.

With these perspectives, two major research objectives were addressed in this investigation. The first involved an experimental assessment of the effects of flooding season and depth in regulating plant community composition and associated edaphic characteristics during initial wetland development within meadows of the DMP. The second was an assessment of the potential for changes in artificial flooding frequencies, seasons and water depth to restore *E. palustris* communities from *T. latifolia*-dominated communities within established wetlands. In essence, this study evaluated the ability of hydrologic treatments to effect plant community change (Cole 1985).

4.2 Materials and Methods

4.2.1 Description of Study Sites

The study was conducted at two created wetland complexes in the DMP region of southern Alberta, including the Kitsim and Contra-Costa wetland complexes (*aka* Kitsim and Contra-Costa, respectively). Both Kitsim and Contra-Costa are located near the city of Brooks (50° 33' N; 111° 51' W) in the DMP region of southern Alberta, Canada. Brooks is an agricultural settlement, relying on irrigation water for primary production. While much of the landscape has been tilled, sizeable native rangelands are used for livestock grazing, wildlife habitat conservation, recreation, and energy extraction.

Created wetlands are flooded using gravity-fed irrigation canals that transport water from holding reservoirs (Appendix XXVIII). By using flood control structures, DUC is capable of regulating the timing and depth of flooding in created wetlands.

Wetland flooding at Kitsim has changed considerably since the inception of the project in 1983. These wetlands were originally flooded three times annually from May to August to maintain permanence. In early 2000, flooding regimes were changed to once a year in August/September (i.e., fall) to reduce wetland permanence, with flooding occurring at depths varying from 30 to 75 cm (Dave Kay, DUC, *pers. comm.*). Overall, the change in flooding practices resulted in an 11% reduction in the proportion of permanent wetlands and an increase of 29% in seasonal or temporary wetlands (Ducks Unlimited Canada, *unpubl.*) based on the classification of Stewart and Kantrud (1971).

In addition to artificial flooding, wetland moisture status is affected annually by spring snow melt and growing season rainfall, as well as evapotranspiration losses. Average long-term (30-year) and annual growing season precipitation and temperature are provided in Appendices I and II, respectively (Environment Canada, *unpubl.*).

4.2.2 Experimental Design and Hydrologic Treatments

A total of 8 and 16 wetlands were selected at Contra-Costa and Kitsim in August 2002, respectively. Wetlands at Contra-Costa were comprised of minimally altered wet or dry meadow communities dominated by *E. palustris*, foxtail barley (*Hordeum jubatum* L.), and western dock (*Rumex occidentalis* S. Wats.), while Kitsim wetlands were heavily dominated by *T. latifolia*.

Hydrologic treatments (flooding at Contra-Costa, and both flooding and drying at Kitsim) were applied to the selected wetlands, and data collected annually from August 2002 to 2005. Independent flooding treatment variables manipulated at Contra-Costa included the season of flooding and depth of flooding (i.e., topographic position) while at Kitsim, they included season of flooding, duration of drying, and depth of flooding.

Under grazing disposition management of the Eastern Irrigation District, both Contra-Costa and Kitsim complexes were annually open to seasonal light to moderate cattle grazing from early summer (June) and mid fall (October).

4.2.2.1 Treatment Implementation at Contra-Costa

New wetland development was assessed at Contra-Costa, where a split-plot design was used to explore relationships among independent and dependent study variables. Season of flooding was the main plot, which was stratified into four depths of flooding (topographic positions) using transects oriented perpendicular to the landscape profile, with repeated annual vegetation and soil sampling from 2002 to 2005.

Season of flooding had three treatment levels, including artificial fall flooding (FF), artificial spring flooding (SF), and continued natural flooding (NF) from spring snow melt and occasional recharge with rainfall. Of the eight experimental wetlands at Contra-Costa, four were assigned to FF, two to SF, and two to the NF treatments. Depth of flooding had four levels, including deep flooding (60 cm), shallow flooding (30 cm), water (flood) line (0 cm), and sub-irrigated upland (-30 cm). To assess the impact of various flooding depths on vegetation and soil characteristics, a 20-m permanently marked transect (with a hand-held GPS) was established within each of the target flooding depths of each wetland (n = 32) (Appendix XXIX). A laser level (Leica Wild LNA 30™) was used to initially establish each transect at the appropriate elevation in the landscape. Wetlands receiving the FF and SF treatments were subsequently flooded until target depths were achieved during August/September 2002 or April 2003, respectively, and repeated annually until September 2004 or April 2005 (Appendix III). Permanent markers (posts) were used to monitor water depth to ensure artificial flooding took place to target levels.

4.2.2.2 Treatment Implementation at Kitsim

A split-plot design was used to explore the relationship between flooding and plant community dynamics at Kitsim. In addition to flooding, the effect of livestock grazing on vegetation responses was assessed. The main plots included four individual wetlands in each flooding treatment (n=16), within which sampling was stratified into ungrazed and grazed areas. A split occurred within the ungrazed /grazed areas into community types stratified by topographic position across the landscape. This was achieved by randomly selecting a portion of each wetland basin and fencing it off with a 25 x 50 m barbed wire exclosure to exclude cattle grazing, which enabled comparison of ungrazed and grazed areas. Each of these, in turn, was stratified into four topographic positions, including sub-irrigated upland, dry meadow, wet meadow and deep marsh zones, as described by Stewart and Kantrud (1971). Permanently marked linear transect (using a hand-held GPS) was established at each topographic position to facilitate repeat annual sampling of herbage and soils throughout the study at Kitsim (n=128). Each transect was oriented perpendicular to the landscape profile.

Independent variables investigated included flooding treatment, cattle grazing and flooding depth (i.e., topographic position). Four flooding treatments were examined, including 2-years of no flooding (or flood cessation) with subsequent fall reflooding (2YNF), 1-year of no flooding with subsequent fall reflooding (1YNF), 8-months of initial drying followed by a change to annual spring flooding (SF), and a continuation of the current practice of annual fall flooding (FF). Wetland flood cessation was implemented to increase the likelihood of *T. latifolia* control via moisture stress.

Of the 16 experimental wetlands, four (replicates) were randomly assigned to each flooding treatment, and implemented from 2002 to 2005 (Appendix IV). All Kitsim study wetlands were set at similar pre-treatment conditions by flooding in either fall 2001 or fall 2002, depending on the treatment. The 2YNF treatment was achieved by deferring artificial fall flooding in both 2002 and 2003, and subsequently reflooding in the fall of 2004. Similarly, the 1YNF treatment was achieved by deferring artificial fall flooding in 2003 and then reflooding in the fall of 2004. The SF treatment was achieved by deferring fall flooding in 2003 to initiate artificial spring flooding starting in 2004. The FF treatment was achieved by continuing with annual artificial fall flooding in August/September (i.e., the regular DUC flooding regime). With the exception of the SF treatment, all Kitsim wetlands were reflooded in the fall of 2004. The SF wetlands were reflooded in spring 2005. The intent of reflooding was to evaluate the impact of all hydrologic treatments through the assessment of post-treatment vegetation responses.

4.2.3. Sampling

4.2.3.1. Dependent Variables

Vegetation sampling focused on two major vegetational groups - native and introduced species, to help understand the potential impacts of hydrology and grazing on the health of rangelands associated with created wetlands in the DMP. By definition, native species included those described as being native to the DMP (Moss 1983, Adams et al. 2005). Introduced species included all others such as naturalized species, weeds and exotic invaders as described by Moss (1983).

Main vegetation (dependent) variables measured in all topographic positions under each treatment combination at both Contra-Costa and Kitsim included:

i. Plant species composition, including percent canopy cover of individual native and introduced species, respectively, and

ii. Richness and diversity of native and introduced species.

Other explanatory variables were measured to understand the relationship of plant community dynamics to flooding (and where applicable, grazing) treatment combinations across the landscapes at Contra-Costa and Kitsim. These included volumetric soil moisture and soil nutrients, such as available nitrogen (nitrates and ammonium) and phosphorus (phosphates). *T. latifolia* root biomass and carbohydrate concentration were assessed in the deep marsh zones of established wetlands at Kitsim to assess changes in the vigor of this species.

Prior to treatment applications, pre-treatment vegetation sampling was conducted in August 2002 on all Contra-Costa wetlands, as well as the 2YNF wetlands at Kitsim. Pre-treatment vegetation sampling on the other Kitsim wetlands was conducted in July

2003. Sampling was conducted at peak growth using eight, 0.25 m^2 (50 x 50 cm) quadrats, systematically placed along each permanent transect for vegetation assessment.

4.2.3.2. Vegetation Sampling

Plant species composition and canopy cover were assessed within all plant communities throughout the sampling years from 2002 to 2005. This was done by identifying and visually estimating the canopy cover of individual species within each of the eight sampling quadrats along the permanent transects. Species composition in each community (i.e., transect) was categorized into two categories, including native and introduced species. Vegetation data were subsequently summarized into species richness (*S*) and Shannon-Wiener diversity indices (*H*) of native and introduced species within each community.

Species richness (*S*) is the simplest measure of community diversity that measures the actual presence or absence of a species, and is a count of the number of different species in a given area (Gaston and Spicer 2004). Richness of native and introduced species in the present study was determined as the number of species per 2 m^2 area, which is the sum area of the eight 0.25 m^2 quadrats along each permanent transect in each topographic position.

The Shannon-Wiener diversity index (*H*) accounts for both abundance and evenness of species within a plant community (Magurran 1988, Rosenzweig 1995). The proportion of species *i*, relative to the total numbers of species (p_i) in each community was calculated, and subsequently multiplied by the natural logarithm of this proportion

($\ln p_i$), which were then summed for all species as outlined in equation (1) below, to obtain diversity indices for the native and non-native species on each transect:

$$H = -\sum_{i=1}^{S} p_i \ln p_i \qquad (1)$$

4.2.3.3. Soil Sampling

Volumetric soil moisture was measured annually from 2003 to 2005 in study wetlands at Contra-Costa and Kitsim in early May (spring), July (early summer) and August (late summer). Two moisture measurements were randomly made along all non-flooded permanent transects using an HH2 Delta-T™ moisture meter with a probe that measured volumetric soil moisture in-situ within 10 cm depth of soil. Flooded transects were considered to be at 100% moisture (i.e., saturation). Moisture sampling could not be conducted in May 2003 and May 2005 due to failure of sampling equipment.

Duplicate soil samples were randomly collected using a soil corer (1.5 cm wide by 10 cm deep) in July along each transect during vegetation sampling for the determination of soil nutrients, including available nitrogen and phosphorus from 2003 to 2005. Pre-flooding soil nutrient sampling was conducted only at Contra-Costa in 2002. Soil samples were promptly air-dried under room temperature and subsequently ground though a 0.5 mm Wiley Mill™. Nutrient analysis was performed at the Natural Resource Analytical Laboratory (NRAL) at the University of Alberta (Department of Renewable Resources).

Available nitrogen was determined as nitrate and ammonium components of air-dried soil samples (Carter 1993). These were extracted by agitating 10 g of air-dried soil in 50 ml of 2M KCl solution for 30 minutes (NRAL Soil Analytical Procedures). The resulting extract was filtered off the solid fraction, and the filtrate analyzed colorimetrically for available nitrogen on a Technicon Flow Analyzer™ at 520 nm for both nitrate and nitrite, and 630 nm for ammonium (Technicon Auto Analyzer II – Nitrate, Nitrite and Ammonium). Available phosphorus was determined using the 'Kelowna Modified Extractable Phosphorus' procedure (Soil and Crop Diagnostic Center of Alberta 1995) by agitating 5 g of air-dried soil in 50 ml of a mixture of 0.015M NH_4F, 1M NH_4OAc, and 0.5M CH_3COOH for 30 minutes (NRAL Soil Analytical Procedures). The resulting extract was filtered off the solid fraction and the filtrate analyzed colorimetrically for available phosphorus on the Technicon Auto Analyzer™ at 880 nm.

4.2.3.4. *T. latifolia* Root Biomass and Carbohydrate Sampling at Kitsim

At the end of all Kitsim treatment applications in 2005, *T. latifolia* root biomass was determined by harvesting *T. latifolia* roots within randomly located 0.25 m^2 quadrats in the deep marsh zones of both ungrazed and grazed locations in all Kitsim study wetlands. Quadrats were harvested by digging as deep as required to remove all *T. latifolia* roots, generally within 30 cm of the soil surface. Duplicate samples were harvested from inside and outside grazing exclosures. After soil was washed off, roots were subsequently oven-dried at 35 °C for 96 hrs and weighed to determine biomass. Roots were then ground through a 0.1 mm Wiley Mill ™ screen and analyzed for energy reserves, including total reducing sugar and starch, at the Ecophysiology Laboratory of the Department of Renewable Resources, University of Alberta. The analytical procedure used was a modified Wienmann Enzymatic Method for removing and analyzing non-structural carbohydrates from plant tissues (Smith 1981).

4.2.4. Statistical Analyses

Due to differences in site characteristics, research questions and study design, the Contra-Costa and Kitsim datasets were analyzed separately. All data were initially tested for normality and found to be normally distributed based on a Shapiro-Wilk test ($P > 0.05$) (SAS Institute Inc. 2003). Pre-flooding species diversity and richness, as well as soil moisture data at Contra-Costa and Kitsim were used as covariates in analyses of vegetation and soils data. Data analyses used ANCOVA for split-plot designs (Steele et al. 1997, Zar 1999) with replicate wetlands within treatment combinations as random factors. *T. latifolia* root biomass and carbohydrate concentration data from the deep marsh zone were analyzed using a 2-way ANOVA for a factorial design (Zar 1999).

Preliminary data analyses indicated no differences in soil moisture content and nutrient concentrations between ungrazed and grazed areas at Kitsim ($P > 0.05$). Hence, soils data are presented for the hydrologic treatments and topographic positions only.

All treatment effects were analyzed using Proc MIXED of SAS (SAS Institute Inc. 2003). Except for statistical hypotheses testing on species diversity and richness, which were considered significant at $P \leq 0.10$, all other statistical tests were considered significant at $P \leq 0.05$ for all main treatment and interaction effects. A one-way ANCOVA (using 2002 pre-flooding cover data as covariate) at 5% level of significance was used to evaluate flooding treatment effects on the end of flooding treatment (2005) relative abundance (canopy cover) of *T. latifolia*, *E. palustris* and all major species (with at least 5% canopy cover) at Contra-Costa. Multiple LSmean comparisons on all significant treatment effects or interactions were performed using Tukey's test ($P \leq 0.05$). Paired t-test was used to evaluate cattle gazing effects within each topographic position on the relative abundance of all major species (with 5% plus cover) at Kitsim following the end of flooding treatments and again after reflooding. Regression analysis was used to explore direct empirical relationships between the relative abundance of *T. latifolia* and *E. palustris*, and soil moisture at Kitsim.

4.3. Results

4.3.1. Soil and Vegetation Responses at Contra-Costa

4.3.1.1. Soil Moisture Dynamics at Contra-Costa

Flooding treatment alone did not affect volumetric soil moisture in each of the three sampling years following the initiation of flooding treatment at Contra-Costa ($P > 0.05$) (Table 4.1). However, there was a significant flooding × topographic position × period of sampling interaction ($P \leq 05$) on soil moisture in each of 2003, 2004 and 2005 (Table 4.1). Detailed examination of these data indicated the spatial distribution of moisture was variable within sampling periods and years ($P \leq 0.05$). As expected, soil moisture was lowest on sub-irrigated uplands in all sampling years, with significantly greater levels in progressively lower topographic positions during each of the sampling periods of May, July and August ($P \leq 0.05$) (Table 4.2). There was an overall temporal decline in soil moisture within each position as the growing season advanced (Table 4.2). While the shallow and deep flooding positions remained similar in moisture prior to the end of July, by August these positions differed from one another in 2003 and 2004.

Differences in soil moisture among flooding treatments varied by topographic position, and were clearly more prominent towards the end of each year. Within uplands, the FF treatment maintained greater moisture, particularly late in the summer, in all 3 years (Table 4.2). At all other positions, the NF treatment had the least soil moisture, with this effect most prominent towards the end of the summer (Table 4.2). While the FF and SF treatments resulted in similar soil moisture throughout 2003, and again prior to August in the following years, the FF treatment had less moisture relative to the SF in August of both 2004 and 2005 (Table 4.2).

4.3.1.2. Soil Nutrient Dynamics at Contra-Costa

With the exception of phosphate ($P = 0.04$), pre-flooding nitrate and ammonium in soils at Contra-Costa were not significant covariates ($P > 0.05$) (Table 4.3).

Nitrate

Soil available nitrate concentration at Contra-Costa was not affected by the flooding treatments implemented ($P = 0.19$) (Table 4.3). Similarly, nitrate concentration did not vary across topographic positions ($P = 0.39$). However, nitrate did vary temporally across sampling years ($P < 0.0001$) (Table 4.3), with an additional flooding treatment × sampling year interaction ($P = 0.02$) (Table 4.3).

Overall, nitrate levels remained similar across all position by flooding treatment combinations (Table 4.4a). Temporal variation in nitrate concentration occurred among flooding treatments, being least on both fall and natural wetlands and greater on spring wetlands in 2003 and 2004 (Table 4.4b). In 2005, all the three flooding treatments experienced significant increases in nitrate concentration ($P < 0.05$), with fall flooding resulting in nearly 4-fold increase (Table 4.4b). Among sampling years overall, nitrate levels remained similar ($P > 0.05$) in 2003 and 2004 but increased significantly in 2005 ($P < 0.05$) (Table 4.4b).

Ammonium

Flooding treatment had no effect on soil available ammonium concentration at Contra-Costa ($P > 0.05$), but displayed a weak interaction with topographic position ($P = 0.06$) (Table 4.3). However, ammonium concentration did vary spatially across topographic positions ($P = 0.01$) and temporally among sampling years ($P = 0.01$) (Table 4.3). Overall, soil ammonium concentrations were lower in uplands than all other positions (Table 4.4a). The flooding by position interaction revealed the presence of spatial variation among ammonium levels due to flood regime (Table 4.4a). In particular, positional differences in ammonium were most pronounced within the FF treatment, followed by the SF, with the fewest differences in the NF treatment (Table 4.4a). Temporally, ammonium concentration declined from the highest level of 19.0 ± 1.5 ppm in 2003 to 14.6 ± 2.6 ppm in 2004 and further to 9.9 ± 0.9 ppm in 2005.

Phosphate

Phosphate concentrations were unaffected by flooding treatment ($P > 0.05$), but varied spatially across topographic positions ($P = 0.02$) (Table 4.3). In addition, there was a significant flooding treatment × topographic position interaction ($P = 0.01$) effect on phosphate concentrations (Table 4.3). Similar to ammonium, phosphate was lowest in the sub-irrigated uplands (Table 4.4a). However, phosphate levels peaked at both the waterline and deep flooding positions, and were intermediate in the shallow flooding zone (Table 4.4a). Minor variations also occurred with respect to the phosphate differences among topographic positions, depending on the flood regime (Table 4.4a).

Soil available phosphate levels were also effected by the year of sampling ($P <$ 0.0001), as well as a year × position effect ($P = 0.04$). While phosphate levels in waterline and deep flooding zones temporally increased from 2003 to 2004, and remained at those levels into 2005, phosphate levels within the upland and shallow flooding zones initially increased from 2003 to 2004, but subsequently declined in 2005 (Table 4.4b).

4.3.1.3. Vegetation Responses at Contra-Costa

Native and Introduced Species Diversity and Richness

Pre-flooding native species diversity and richness were not significant covariates ($P > 0.05$) at Contra-Costa (Table 4.5). Pre-flooding introduced species diversity was a significant covariate ($P = 0.03$) while richness was not ($P = 0.17$).

Flooding treatment did not affect native species diversity or richness ($P > 0.5$) (Table 4.5). These parameters rather varied across topographic positions ($P = 0.0001$) and sampling years ($P < 0.1$) (Table 4.5).

Overall differences among positions indicated that native species diversity and richness were generally greatest on uplands, with a progressive decline towards lower elevations [Table 4.6a (i)]. Temporally, native species diversity and richness decreased from 2003 to 2004, with a subsequent increase in 2005 [Table 4.6a (ii)].

Introduced species diversity and richness were not affected by flooding treatment at Contra-Costa ($P > 0.1$) (Table 4.5). Similarly, these variables did not vary spatially across topographic positions in the landscape ($P > 0.1$). However, measures of introduced species diversity and richness exhibited temporal variation from 2003 to 2005 from a year effect ($P \leq 0.1$) (Table 4.5). On average, introduced species diversity at Contra-Costa remained similar between 2003 and 2004, but increased significantly ($P < 0.05$) in 2005 (Table 4.6b). In contrast, introduced species richness declined from 2003 to 2004 before subsequently increasing to its greatest value in 2005 (Table 4.6b).

Plant Species Composition

Following artificial flooding at Contra-Costa, vegetation differences from the flood regime varied depending on topographic position. Overall, native and introduced species in upper topographic zones (both the upland and waterline zones) had a canopy cover of approximately 90% and 5%, respectively. Within the upland (Table 4.7a) position, the abundance of many native species changed in response to flooding. For example, *H. jubatum* was positively affected by artificial flooding, regardless of season. Other species were positively impacted, either by FF (e.g., *P. palustris, S. comata*) or SF (*A. scabra*, *B. gracilis*) treatments from 2002 to 2005 (Table 4.7a). Species that were negatively impacted within uplands by artificial flooding, regardless of season, included *A. smithii* and *C. filifolia* (Table 4.7a). *C. utriculata* and *A. smithii* were reduced to a greater extent by FF, rather than SF. *S. densa* appeared negatively impacted by all flooding treatments investigated. Comparison of species response among flooding treatments in 2005 indicated that artificial flooding led to a greater reduction in the relative abundance of some native species on uplands, e.g., *A. smithii* and *C. filifolia*, with fall flooding causing the greatest reduction (Table 4.7a). On the other hand, the relative abundance of many native and introduced species on uplands increased with artificial flooding, including both FF and SF treatments (Table 4.7a).

Within the waterline zone of the landscape (Table 4.7b), only native species responded to flood regime. At end of flooding treatment implementation in 2005, the relative abundance of *P. palustris* was less under both FF and SF treatments compared to that of NF (Table 4.7b). The relative abundance of *A. smithii* was greatest on SF wetlands and least on NF wetlands. While the relative abundance of *M. arvensis* was least on FF wetlands, that of *A. scabra* was least on SF wetlands. Notably, *E. palustris* in the waterline zones increased with artificial flooding, especially under FF treatment.

The most marked overall changes in vegetation composition at Contra-Costa appeared to occur in the shallow flooding (Table 4.7c) and deep flooding (Table 4.7d) zones. The relative abundance of several native species in both of these positions was distinctly enhanced by artificial flooding, regardless of the timing of flooding (Tables 4.7c and 4.7d). For example, *E. palustris* increased in abundance following the implementation of FF and SF treatments in both the shallow flooding (Table 4.7c) and deep flooding (Table 4.7d) zones from 2002 to 2005: the increase in shallow flooded zones represented a 3 to 4-fold increase. Deep flooded zones remained predominantly *E. palustris* throughout the study. Notably, there was also a near 3-fold increase in the coverage of *E. palustris* within deep flooding zones of NF wetlands during the study period from 2002 to 2005 (Table 4.7d), although this increase did not extend to shallow flooding zones of the NF treatment over the same period (Table 4.7c). Other species that increased with artificial flooding included *A. aequalis* at the shallow flooding position, but only within the SF treatment (Table 4.7c).

Artificial flooding led to declines or the loss of several native species in both the shallow and deep flooding zones (Tables 4.7c and 4.7d). Deep flooding under either a FF or SF treatment led to the complete displacement of *B. syzigachne, H. jubatum*, and *R. occidentalis*. *A. smithii* and *M. arvensis* were similarly eliminated within the shallow flooding zone under both artificial flooding treatments. Within this landscape position, *B. syzigachne* and *P. palustris* were nearly displaced (Tables 4.7c and 4.7d).

Three years of artificial flooding in both the SF and FF treatments led to the removal of all introduced species initially present, such as *C. arvense, C. album, P. pratense* and *M. lupulina*, within each of the shallow flooding (Table 4.7c) and deep flooding (Table 4.7d) zones. However, these same flood regimes facilitated the entry of *T. latifolia* during this period. *T. latifolia* was originally absent in the shallow flooding zones of FF and SF wetlands, as well as the deep flooding zones of NF wetlands in 2002. By 2005, the relative abundance of *T. latifolia* in shallow flooded zones of both the FF and SF wetlands increased to 2.4 and 8.7%, respectively (Table 4.7c). In contrast, the only increase in this species at the deep flooding position occurred within the NF treatment (Table 4.7d).

4.3.2. Soil and Vegetation Responses at Kitsim

4.3.2.1. Soil Moisture Dynamics at Kitsim

Volumetric soil moisture at Kitsim was affected by flooding treatment in 2003 and 2004 ($P \leq 0.05$), but not 2005 ($P > 0.05$) (Table 4.1). However, there was a flooding treatment × topographic position × period of sampling interaction ($P \leq 0.05$) on soil moisture in each of the three sampling years (Table 4.1).

Similar to observations at Contra-Costa, soil moisture levels were lowest on uplands at Kitsim, and progressively declined ($P \leq 0.05$) with elevation through the dry meadow, wet meadow, and into the deep marsh zones (Table 4.8). Additionally, soil moisture decreased seasonally, reaching their lowest levels in August (Table 4.8).

The interaction of flooding, position and sampling period indicated complex patterns of spatial and temporal variation in soil moisture at the Kitsim location. Across topographic positions and sampling periods, soil moisture content was generally lowest on the flood cessation wetlands (1YNF and 2YNF treatments), which became most evident as the growing season advanced into early July and then mid August (Table 4.8). While few differences in soil moisture existed between the FF and SF treatments within the wet meadow and deep marsh zones, these treatments did exhibit differences in the two more elevated positions, particularly later in the summer when the FF treatment tended to be greater at times (Table 4.8).

In 2005 following the return of annual flooding, moisture levels were generally greater than the year before but continued to exhibit spatial differences among topographic positions (Table 4.8). Despite ongoing depletion of soil water throughout the summer, uplands continued to remain lower in soil moisture compared to all other positions in mid August. Within positions, however, differences among the various flooding treatments were minimal, even at the end of the summer (Table 4.8).

4.3.2.2. Soil Nutrient Dynamics at Kitsim

Nitrate

Flooding treatment did not affect soil available nitrate concentrations ($P = 0.7$) at Kitsim (Table 4.3). However, nitrate concentration did vary spatially across topographic positions ($P = 0.005$) and temporally among sampling years ($P < 0.0001$) (Table 4.3). In addition, nitrate was affected by the interaction of topographic position and sampling year ($P = 0.0001$) (Table 4.3).

Overall nitrate levels were lower on the upland and dry meadow locations compared to the wet meadow and deep marsh zones (Table 4.9a). On average, nitrate levels were lowest at the end of flooding treatment in 2004 and greatest following reflooding in 2005 (Table 4.9a). The interaction of year with position reflects temporal variation from 2003 to 2005 in the spatial differences of nitrate across the landscape. During 2003, both the upland and deep marsh zones were lower in nitrate than the wet meadow zone (Table 4.9a). At the end of flooding treatment in 2004, nitrate levels were generally low and similar across all topographic positions (Table 4.9a). However, with post treatment reflooding, nitrate levels during 2005 in the wet meadow and deep marsh zones increased to levels above that of the upland and dry meadow zones, with the lowest nitrate concentration in the dry meadow zones (Table 4.9a).

Ammonium

Soil ammonium concentration at Kitsim was affected by flooding treatment ($P = 0.003$), as well as varied across sampling years ($P = 0.001$) (Table 4.3). Although there was no isolated topographic position effect ($P > 0.05$), ammonium was also affected by both flooding × sampling year ($P = 0.002$) and flooding × topographic position × sampling year ($P = 0.0003$) effects, indicating soil ammonium levels varied among flooding treatments both temporally and spatially during the study (Table 4.3).

During the early stages of each flooding treatment in 2003, soil ammonium was greatest within the 1YNF treatment, followed by the SF, 2YNF and then the FF treatments (Table 4.9b). One year later during the last year of treatment, the 1YNF and 2YNF remained greater than the SF, which in turn, was greater than the FF (Table 4.9b). With reflooding of all wetlands in 2005, ammonium levels were similar among the FF, 1YNF and 2YNF treatments, with only the FF having greater soil ammonium than the SF treatment (Table 4.9b). Within flooding treatments, soil ammonium levels were highly variable among topographic positions, with additional differences due to the year of sampling. For example, while no differences in soil ammonium were evident among positions in the FF treatment in 2003, with reflooding, the wet meadow and deep marsh areas had greater ammonium in 2005 than the other two positions (Table 4.9b). Within the 1YNF treatment, soil ammonium initially declined with increasing elevation in the landscape in 2003, became more stable among positions in 2004, and then increased with elevation in 2005 after reflooding (Table 4.9b). In contrast, the 2YNF treatment exhibited a markedly different pattern, with the lowest soil ammonium in the deep marsh zone during 2003, and relatively stable ammonium levels by 2005,

Phosphate

Soil phosphate concentrations at Kitsim were affected neither by flooding treatment nor topographic position ($P > 0.05$) (Table 4.3). However, phosphate concentrations did vary temporally across sampling years ($P = 0.001$). Soil phosphate levels were lowest in 2003 (10.6 ± 1.1 ppm), increased ($P < 0.05$) to 15.3 ± 0.8 ppm in 2004, and subsequently declined ($P < 0.05$) to 13.1 ± 0.6 ppm in 2005.

4.3.2.3. Vegetation Responses at Kitsim

Pre-flooding diversity and richness data had a significant covariate effect ($P < 0.0001$) on most of native richness and diversity measures examined (Table 4.10). Similarly, pre-flooding introduced species diversity and richness were significant covariates for all measures of introduced species abundance ($P < 0.001$) during both the end of flooding and post-reflooding periods (Table 4.10).

Native and Introduced Species Diversity and Richness

After administration of the flooding treatments, the presence of cattle grazing and topographic position affected native species diversity and richness ($P \leq 0.05$), with flooding treatment having no impact ($P > 0.10$) on either one (Table 4.10). While none of these 3 main factors (flooding, grazing, or position) had any effect on native species diversity following post-treatment reflooding ($P > 0.10$) (Table 4.10), both flooding treatment and topographic position, as well as their interaction, affected native species richness at that time ($P \leq 0.05$) (Table 4.10).

Immediately after the completion of flooding treatment implementation in 2004, ungrazed areas had both greater native species diversity and richness compared to grazed areas ($P = 0.04$). Average native species diversity in ungrazed areas was 1.21 ± 0.03

while that of grazed areas was 1.11 ± 0.03. Similarly, native species richness in ungrazed areas was 7.6 ± 0.2 species /2m^{-2}, with that of grazed areas being 6.7 ± 0.2 species /2m^{-2}.

Spatial patterns in native species diversity and richness across the landscape at the end of flooding closely paralleled each other, being greatest in uplands and lowest within the deep marsh zone (Table 4.11a). While no positional differences in native species diversity were evident following post-treatment reflooding, trends in native species richness indicated that the deep marsh zone remained lower in mean richness than all other positions (Table 4.11a). Among the flooding treatments overall, the SF treatment had greater richness than both the FF and 2YNF treatments (Table 4.11a). However, this pattern varied among positions, with no differences among flooding treatments at either the dry meadow or wet meadow positions. Within uplands, FF had lower native richness than the 1YNF treatment, while at the deep marsh location, FF and SF treatments had fewer native species than the 2YNF treatment (Table 4.11a).

Unlike native species, introduced species diversity and richness were affected by flooding treatment in all sampling periods ($P < 0.10$), with an additional affect of position at all times of sampling ($P < 0.01$) (Table 4.10). In addition, the interaction of flooding x position affected introduced diversity and richness during the end of flooding treatment sampling periods ($P = 0.10$), as well as introduced diversity following post-treatment reflooding sampling ($P = 0.03$). Grazing, either alone or with other treatment effects, had no effect ($P > 0.10$) on introduced species throughout the study (Table 4.11a).

Across topographic positions, both introduced species diversity and richness were generally greatest at the dry and wet meadow positions, followed by the deep marsh locations (Table 4.11b). In contrast, uplands had a low presence of introduced species as characterized by both richness and diversity measures (Table 4.11b). Overall flooding treatment effects consistently indicated a tendency for lower introduced species diversity and richness to occur in the FF treatment compared to all others, with the 2YNF treatment additionally greater in introduced species diversity compared to the SF and 1YNF at the end of implementation of the flooding treatments (Table 4.11b). Moreover, increases in introduced species diversity and richness were most pronounced in the dry meadow, wet meadow or deep marsh zones with the presence of flood cessation within either the 1YNF or 2YNF wetlands (Table 4.11b).

Plant Species Composition

Compared to flood cessation (i.e., 1YNF and 2YNF treatments), seasonality of flooding (i.e., FF and SF treatments) less impacted vegetation composition and relative abundance (canopy cover) across the four topographic positions assessed over the course of the study. Thus, vegetational changes on fall and spring flooded wetlands are presented in Appendices X to XVII.

Vegetation changes in the upland and dry meadow zones of 2YNF wetlands (Tables 4.12a and 4.12b) and 1YNF wetlands (Tables 4.12e and 4.12f) following the implementation of flooding treatments at Kitsim reveal a number of key trends, some of which extend into the lower landscape positions. Summaries of the native and introduced plant species composition at the wet meadow and deep marsh positions within each of the flooding treatments are provided in Table 4.12c and Table 4.12d for 2YNF wetlands, and Table 4.12g and Table 4.12h for 1YNF wetlands.

Within uplands, *A. smithii* declined in both the 2YNF (Table 4.12a) and 1YNF (Table 4.12e) treatments, only to promptly recover with reflooding. Other native species like *S. densa* declined on uplands under drying, with only partial recovery upon reflooding. A similar trend was found for *A. frigida* within the 2YNF wetlands (Table 4.12a) and *C. filifolia* within the 1YNF wetlands (Table 4.12e). In both of these flooding treatments, flood cessation allowed the introduced grass *P. pratensis* to increase markedly on uplands, which then declined with subsequent reflooding.

Vegetation changes at the dry meadow zone in response to flood cessation included similar reductions in *A. smithii* (Table 4.12b; Table 4.12f), although unlike the trend observed in uplands, this species remained low with reflooding. Minor reductions in *C. rostrata* and *P. palustris* were evident with temporary drying of dry meadows in the 1YNF treatment (Table 4.12f), while *H. jubatum* declined in the 2YNF treatment (Table 4.12b). A similar reduction in *R. occidentalis* was evident in the 2YNF treatment (Table 4.12b), which was also evident in wet meadows of this same treatment (Table 4.12c).

At the wet meadow zone, few native species demonstrated increases in relative abundance, and these increases occurred only with post-drying reflooding. Species that increased include *E. glandulosum* in the 2YNF (Table 4.12c) and *C. utriculata* in the 1YNF (Table 4.12g). Similar to that observed at the dry meadow zone, *R. occidentalis* declined with both drying and reflooding in wet meadows of the 2YNF (Table 4.12c), although this same species increased markedly with drying of the deep marsh zone in both the 1YNF (Table 4.12h) and 2YNF (Table 4.12d) wetlands.

Other native species responding to flooding in the deep marsh zone included *H. jubatum*, which increased with reflooding in the 2YNF (Table 4.12d), and *E. palustris*, which declined with drying in 1YNF wetlands, only to promptly increase with reflooding (Table 4.12h). Levels of *E. palustris* in wet meadows of the 1YNF remained relatively stable throughout the study (Table 4.12g), and this species was relatively sparse in all dryer topographic positions.

There were overall fewer species in the deep marsh zones compared to the wet meadow zones across the Kitsim study area. After administering the 'drying' treatments through 2004, both the 2YNF and 1YNF treatments facilitated the re-establishment of several native species in the deep marsh zone that were absent during pre-treatment sampling. These species included *A. millefolium, B. syzigachne, E. glandulosum, E. aspermum, H. jubatum, P. amphibium, and R. occidentalis*. Similar results were evident in the wet meadow zones, where species like *B. syzigachne*, *P. palustris* and *P. fruticosa* appeared. However, subsequent post-treatment re-flooding resulted in marked declines in the abundance of many of the species that increased in the deep marsh zone, or occasionally their removal, including *A. millefolium*, *E. aspermum*, and *E. glandulosum.*

The 1YNF and 2YNF treatments also facilitated the establishment and/or increase of introduced species in the wet meadow and deep marsh zones at the end of flooding treatment implementation. Within dry meadows of the 1YNF and 2YNF, the noxious weed *S. arvensis* increased with drying, and either remained high or increased further through reflooding (Table 4.12b; Table 4.12f). *S. arvensis* also exhibited a marked increase to drying within wet meadows of the 2YNF (Table 4.12c), and although it declined with reflooding, this species remained abundant. At the deep marsh position, *S. arvensis* was abundant in both the 2YNF treatment following drying (Table 4.12d) and in the 1YNF treatment following reflooding (Table 4.12h).

A similar trend was evident for *C. arvense*, which increased with flood cessation in dry meadows of the 2YNF and remained elevated (Table 4.12b), a finding in sharp contrast to the 1YNF where *C. arvense* remained abundant during drying but promptly declined with reflooding (Table 4.12f). While increases in *C. arvense* were minimal at the wet meadow (Table 4.12g) and deep marsh zones (Table 4.12h) of the 1YNF, this species increased prominently with drying and remained abundant in wet meadows of the 2YNF (Table 4.12c).

The abundance of *T. latifolia* was also clearly impacted by the flooding treatments. The 2YNF treatment resulted in approximately 90% reduction in the relative abundance (% cover) of this species within the wet meadow (Table 4.12c) and deep marsh (Table 4.12d) zones after implementing flood cessation. Moreover, the 2YNF treatment also affected the subsequent recovery of *T. latifolia* during reflooding, as evidenced by the minimal recovery at that time. Similar reductions in *T. latifolia* were observed in the 1YNF treatment, where this species underwent a 57% and 74% relative decline in canopy cover within the wet meadow (Table 4.12g) and deep marsh (Table 4.12h) zones, respectively, at the end of treatment implementation. However, unlike the 2YNF treatment, *T. latifolia* exhibited a greater degree of recovery following post-treatment reflooding within the 1YNF treatment.

There were also isolated differences in the relative abundance of individual plant species due to the presence and absence of grazing within various topographic positions of the 2YNF and 1YNF treatments. For example, uplands of the 2YNF treatment grazed by cattle were greater in *A. smithii* and *C. filifolia*, but lower in *S. comata* (Table 4.12a). Within 1YNF wetlands, only *A. pectiniforme* was greater with cattle grazing (Table

4.12e). Within dry meadows of the 2YNF treatment (Table 4.12b), grazed areas appeared to have greater *A. smithii* and *P. palustris*, as well as *C. arvense*, but reduced levels of *P. pratensis* and *S. arvensis* (Table 4.12b). While few species appeared to be affected by cattle presence in wet meadows of the 1YNF wetlands (e.g., *H. jubatum* increased and *C. utriculata* decreased) (Table 4.12g), more species were impacted by cattle presence within the 2YNF wetlands (Table 4.12c). For example, *E. glandulosum*, *H. jubatum*, and *P. palustris* all increased under grazing at the end of the study (Table 4.12c). However, *Lactuca* species remained lower under grazing (Table 4.12c). Additionally, *C. arvense* cover at the end of drying was greater in wet meadows of the 2YNF wetlands exposed to cattle grazing.

Finally, grazing also had a significant impact on several plant species within the deep marsh zones of the flood cessation wetlands at Kitsim. Grazing increased the abundance of *R. occidentalis*, either at the end of drying within the 1YNF treatment (Table 4.12h) or after reflooding within the 2YNF treatment (Table 4.12d). Grazing also decreased the abundance of *E. palustris* at the end of drying within the 1YNF treatment (Table 4.12h). Levels of *T. latifolia* were also affected by grazing, with lower levels under grazed conditions in both the 1YNF and 2YNF treatments at the end of the study. Lastly, grazing within the 2YNF treatment also increased the abundance of *S. arvensis* at the end of drying (Table 4.12d).

T. latifolia Root Biomass and Carbohydrate Concentration

While cattle grazing had no impact on *T. latifolia* root biomass at Kitsim ($P > 0.05$) after reflooding in 2005, this parameter was affected by flooding treatment ($P =$

0.03). Specifically, the 2YNF treatment resulted in the least *T. latifolia* root biomass, followed by the 1YNF, SF and FF treatments (Fig. 4.2). Proportional biomass allocation data indicated that *T. latifolia* rhizomes consistently contributed about 73% of the total root biomass, with only 27% allocated to the crown (Fig. 4.2).

Flooding treatment had no effect on either the concentration of total free sugars or starch, within *T. latifolia* crowns and rhizomes ($P > 0.05$). Overall mean rhizome sugar and starch concentrations were 171 ± 12.8 and 118 ± 20.2 ppm, respectively. While cattle grazing did not affect rhizome sugar and starch concentrations ($P > 0.05$), cattle grazing did affect the concentration of total free sugar ($P = 0.006$) and starch ($P = 0.005$) concentrations within *T. latifolia* crowns harvested from individual plant communities. Crown free sugar and starch concentrations were lower in grazed areas (Fig. 4.3), representing reductions of 17.3 and 29%, respectively, compared to ungrazed areas.

4.3.3. Relationship of *T. latifolia* and *E. palustris* Cover to Soil Moisture at Kitsim

Following end of flooding treatment implementation in 2004, *T. latifolia* canopy cover in established wetlands at Kitsim was significantly related to minimum soil moisture ($P = 0.0003$) (Fig. 4.4A). Within the Kitsim wetlands, about 55% soil moisture appears to coincide with 100% *T. latifolia* coverage of affected wetlands. Notably, the relationship in Fig. 4.4A indicates that *T. latifolia* canopy cover can be reduced to a minimum at approximately 5% soil moisture.

The relationship of *E. palustris* cover to soil moisture within the Kitsim study wetlands indicated no significant relationship with soil moisture ($P = 0.19$). However, graphical interpolation suggested that increasing soil moisture above 50% may subsequently lead to complete *E. palustris* eradication within affected wetlands (Fig. 4.4B). Similarly, reducing soil moisture appears to be less favorable for *E. palustris* (Fig. 4.4B). Although minimal in coverage, *E. palustris* appeared to optimally survive in *T. latifolia* infested wetlands at about 20-25% moisture (Fig. 4.4B).

4.4. Discussion

Plant communities can have ecological thresholds that if exceeded, result in transition to alternative states (Briske et al. 2006). Various forms of disturbance such as fire, grazing and weather can trigger plant community succession in naturally occurring landscapes (Fuhlendorf and Smeins 1997, Fuhlendorf et al. 2001, Boer and Stafford-Smith 2003, Briske et al. 2006). A novel result of the present study is the finding that anthropogenic flooding within created prairie wetlands is an important disturbance regime that appears to result in markedly altered community succession, which extended over a prolonged time period, may be difficult to reverse, at least with short-term drying. The inability of the present disturbance-induced vegetation within older established wetlands to revert to pre-disturbance vegetation with the removal of anthropogenic flooding may be due to the fact that anthropogenic flooding caused ecological threshold to be exceeded, and facilitated the invasion of a competitive disturbance-tolerant species.

4.4.1. Plant Community Succession on Newly Created Wetlands

Plant community dynamics on newly flooded artificial wetlands at Contra-Costa indicated strong spatial variation in native species diversity and richness across topographic positions, with sub-irrigated uplands being more diverse and rich in native species than deep flooding topographic zones. As might be expected, increased flooding, as occurred within the FF and SF treatments, led to community simplification, often to near monotypic stands in the shallow and deep flooding zones, with dominance by only a few hydrophytic species, particularly *E. palustris*. The prompt initial succession to *E. palustris* communities regardless of seasonality of flooding parallels that of earlier observations by Millar (1973) and Sankowski et al. (1987) where initial flooding of prairie lowlands in southern Saskatchewan and Alberta led to large increases in the relative abundance of this species. The pattern of initial secondary succession documented here raises a fundamental question as to why short term flooding leads to domination by *E. palustris*.

The successional transition of wetlands may be facilitated by the availability of viable plant propagules, as well as the suitability of new ecosystem conditions favorable to the transitional species (Mitsch and Gosselink 2000). It is likely that *E. palustris* has a high presence in the soil seed bank of affected wetlands, which enabled this species to rapidly establish with initial flooding (Sankowski et al. 1987). Although the exact origin of *E. palustris* propagules remains unknown, seeds of this species may have remained dormant under dry conditions for a long time, and awaited the emergence of favorable environmental conditions. The ideal hydrologic conditions for *E. palustris* during initial flooding at Contra-Costa appeared to coincide with the shallow and deep flooding zones, which were moister, and held moisture longer into the summer. However, the ephemeral, opportunistic responsiveness of *E. palustris* to flooding was also evident at Contra-Costa within the NF treatment, in which the relative abundance of this species fluctuated between 30 and 72% over the course of the study, presumably in response to changes in yearly rainfall and temporary flood levels. The final study year of 2005 was particularly wet during the growing season, and led to prolonged flooding of wetlands, even the NF treatments. Several other plant species similarly increased in the NF wetlands at that time, including *B. syzigachne* and *P. palustris*, which together with abundant *E. palustris*, appeared to displace *H. jubatum* and *R. occidentalis*.

Overall native species diversity and richness in deep flooding zones declined with time since the implementation of artificial flooding, and indicated rapid succession from a more diverse community to a simple community. This observation conforms to that of Shaffer et al. (1992), who observed a temporal decline in species diversity within lower topographic zones of wetlands in Delta, Louisiana, USA. They attributed the declines to combined effects of nutria (*Myocaster coypus*) grazing and prolonged flooding. However, decreases in native species diversity and richness documented here are more likely due to flooding alone, as the effect of cattle grazing was minimal because of low stocking rates during the present study.

Many native plant species in the upland topographic position responded to flooding in adjacent wetlands, with these responses highly variable depending on the plant species and the season of water addition. As upland transects were established 30 cm above the waterline, changes in species composition at this location were likely facilitated by sub-irrigation influences. Plants in the Dry Mixed Grass prairie region typically have roots extending to at least 50 cm, and often well over 1 m in depth (Coupland and Johnson 1965), suggesting they were likely able to access the water table associated with the adjacent wetland. However, the increased moisture would not be evident in the moisture sampling conducted, which was limited to the top 10 cm of soil.

Artificial flooding reduced the abundance of several common native rangeland plants on uplands, including *A. smithii* and upland sedges (e.g., *C. filifolia*). As both of these species are tolerant of relatively dry soil conditions, the reductions in these species may be associated with increased competition from species that increased with flooding during spring (*A. scabra*, *B. gracilis*), fall (*C. utriculata*, *P. palustris*, *S. comata*), or either (*H. jubatum*) season. Several of these species (*A. scabra*, *P. palustris* and *H. jubatum*) are opportunistic species preferring abundant moisture, while *B. gracilis*, a warm season, relatively shallow-rooted grass, may benefit from increased moisture availability during July, a time when moisture is particularly limiting for growth in the Dry Mixed Grass Prairie region (Willms and Jefferson 1993).

While several plant species responded differentially to spring and fall flooding, including *A. smithii*, *B. gracilis*, *Carex* spp., *H. jubatum*, *P. palustris*, *S. densa*, and *S. comata*, no direct explanation could be made for these results. However, differences in the relative timing of root growth and soil moisture use among species, coupled with differences in the relative availability of water under fall and spring flooding, may account for these differences (Coupland and Johnson 1965, Schenk and Jackson 2002).

Contrary to the expectation that anthropogenic disturbances may facilitate exotic invasion into native ecosystems (Milchunas et al. 1990, Wilcox and Thurow 2006), results from the recently initiated flooding on wetlands at Contra-Costa indicated no differences in introduced species diversity and richness across topographic positions, with very limited invasion by noxious weeds (e.g., *S. arvensis*) on uplands and at the waterline position under FF treatment. Although it may be too early in the flooding process to fully assess introduced species patterns, it is possible that the prompt development of closed canopy *E. palustris* communities prevented invasion of these species, particularly within the lower topographic zones. Continued flooding may lead to successional development of a more resistant *T. latifolia* community. Evidence of this was observed in the relative abundance of *T. latifolia*, which although originally absent in study wetlands at Contra-Costa, began to appear within as little as two years of initial flooding. Although the initial source of this species is unknown, it is likely that *T. latifolia* propagules were deposited into the artificial wetlands through flood water, wind or animal movement. *T. latifolia* propagules also appeared to be present in the original natural wetland basin soils, awaiting the emergence of a more favorable condition to become established, as evidence by the emergence of *T. latifolia* within the NF wetlands at the deep flooding zone.

In addition to extended flooding, *T. latifolia* has been reported to utilize nutrient enrichment (particularly elevated phosphorus) as a mechanism for competitively displacing less aggressive plant species from wetlands (Urban et al. 1993, Newman et al. 1996, Weng et al. 2006). Nutrient data from landscapes associated with newly developed wetlands at Contra-Costa supported this assertion. The study results indicated that ammonium replaced nitrates within flooded lower topographic zones, similar to Mitsch and Gosselink (2000), with ammonium levels temporally declining in flooded zones. This finding leads one to theorize that productive plants like *E. palustris* responded to the high initial ammonium levels arising from reduced soil conditions under flooding (Rejmankova et al. 1995, Mitsch and Gosselink 2000, Sorrell et al. 2002), which it subsequently utilized, leading to ammonium depletion with continued flooding in subsequent years.

Alongside the temporal reduction in ammonium there was an increase in phosphate concentration within flooded zones. Mitsch and Gosselink (2000) have indicated that phosphorus levels increase under reduced soil conditions with flooding, and can be actively taken up by several flood-tolerant species, including *T. latifolia* (Weng et al. 2006). Availability of nitrogen, rather than phosphorus, is capable of limiting *E. palustris* growth (Sorrell et al. 2002), and it is likely that nitrate and ammonium uptake and temporal depletion in the flooded wetlands may produce a negative feedback on this species by inhibiting its subsequent growth, and thereby lend the plant to competitive displacement by species more adapted to the new ecosystem conditions (e.g., *T. latifolia*). With increasing accumulation of phosphorus in subsequent years of flooding, it is also likely that the newly emerging phosphate-rich anoxic wetland ecosystem set the stage for successional transition to *T. latifolia* (Weng et al. 2006). Thus, the temporal increase in phosphorus in lower topographic positions may combine with increased soil moisture to facilitate initial *T. latifolia* invasion, which may lead to the displacement of *E. palustris*, such as that evident at Kitsim.

The results of the Contra-Costa study indicated that soil moisture temporally declined across all topographic positions as the growing season advanced. The declining temporal trend in soil moisture suggests that under carefully regulated flooding, newly created wetlands in the Dry Mixed Grass Prairie may be managed to assume ephemeral or seasonal wetland status (Kantrud 1992) if artificial flooding is periodically curtailed. It is therefore possible that such natural drawdown cycles may prevent the sustenance of anoxic conditions that exert a great influence on soil nutrient dynamics, particularly nitrogen depletion and phosphorus accumulation (Mitsch and Gosselink 2000), and thus prevent the susceptibility of intermediate *E. palustris* communities to competitive displacement by *T. latifolia* (Millar 1973). Finally, the incorporation of natural drawdown cycles may help increase and maintain native plant species diversity and richness, which in turn, may be effective in reducing wetland nutrient levels through phytoremediation (Doub 2000), thereby offsetting the influence of phosphorus accumulation from previous flooding. Under this scenario, intermittent (i.e., discontinuous) artificial flooding may more likely help maintain mid-successional *E. palustris* communities that provide the preferred habitat type for Pintail and forage for livestock.

4.4.2. Plant Community Changes Within Established Wetlands

Landscape patterns of native species diversity and richness on established wetlands paralleled that of newly developed wetlands, being greatest on uplands and declining towards deep marsh zones, where floristically simple communities dominated. However, unlike at Contra-Costa where *E. palustris* dominated newly flooded areas, established wetlands at Kitsim were predominantly *T. latifolia*. The marked abundance of *T. latifolia* in deep marsh zones reinforces the ability of this species to competitively exclude other species, including *E. palustris* (Grace and Wetzel 1981, Swanson 1992).

Among the flooding treatments investigated, fall and spring flooding produced similar effects, including maintenance of few native species, particularly in deep marsh zones. This occurred because neither of these flooding treatments was able to control *T. latifolia* in deep marsh zones, and the species persisted as near monotypic stands of vegetation in established wetlands rendered less habitable by *E. palustris*. Thus, extended flooding led to the maintenance of a more stable and resistant *Typha*-dominated community, which parallels observations made elsewhere (Millar 1973, Grace and Wetzel 1981, Swanson 1987, Swanson 1992, LaBaugh and Swanson 1992, Newman et al. 1996).

Results of the flood cessation treatments indicated that although *T. latifolia* is resistant to extreme moisture stress (Chapter 3), its relative abundance may be reduced with flood cessation. One year of flood cessation was less effective in inducing changes in *T. latifolia* community, likely because soil moisture levels failed to fall anywhere near the 5% level needed to induce high mortality in this species (Chapter 3). In contrast, however, flood cessation for up to two years led to significant changes within these *Typha*-dominated communities of the wet meadow and deep marsh zones. Two years of flood cessation not only reduced the relative abundance (i.e., cover) of *T. latifolia* but also increased the diversity and richness of native species in deep marsh zones where *T. latifolia* initially dominated.

T. latifolia relative abundance was closely correlated to soil moisture within wetlands receiving the 2 years flood cessation. Moreover, complete *T. latifolia* eradication appeared to require soil moisture levels to fall to 5% or less through soil drying. This quantitative threshold value corroborates with what was determined experimentally under controlled conditions in the greenhouse experiment (Chapter 3). However, minimum field moisture levels attained under actual field conditions in the wet meadow and deep marsh zones of the 2 year flood cessation wetlands at Kitsim in August 2004 were 13.8 and 19.0%, respectively. Compared to the required 5% moisture threshold, it appears highly unlikely that *T. latifolia* can be eradicated from affected wetlands with only 2 years of flood cessation, particularly with ongoing moisture recharge from growing season precipitation. As a result, these wetlands would need longer than 2 years of flood cessation to achieve a substantial and long-term reduction in *T. latifolia,* and may also require coincidental periods of climatic drought to bring soil moisture down to levels detrimental to this species. *T. latifolia* also promptly re-colonized the 1YNF and 2YNF wetlands following post-treatment reflooding, suggesting that this species has high resilience to drought conditions. Thus, *T. latifolia* continued to dominate affected wetlands, even after two years of flood cessation.

In addition to facilitating the return of some native species, flood cessation also facilitated the invasion of introduced species. Introduced species diversity and richness increased temporarily (i.e., during the drying period), particularly within the dry and wet meadow zones of the SF, 1YNF and 2YNF wetlands. Apart from *T. latifolia*, the most prevalent among introduced species in low-lying topographic zones were two disturbance-induced noxious weeds – *C. arvense* and *S. arvensis*. Although the flooding treatments resulted in changes in once stable *T. latifolia*-dominated communities in the deep marsh zones, it also led to the development of both native and introduced species, all to the exclusion of the desired *E. palustris* community. The present results suggest that inducing wetland community change with the removal of artificial flooding may not guarantee restoration of the desirable (*E. palustris*) community, but instead, may favor invasion by more opportunistic, disturbance adapted species. Also, once *E. palustris* is completely displaced by T. *latifolia*, it is unlikely to be restored soon after reflooding. This may be due to temporary loss of *E. palustris* propagules or the attainment of ecological thresholds (e.g., elevated phosphorus) detrimental to its growth. This phenomenon may be described as a major setback to effective restoration of degraded ecosystems (e.g., Briske et al. 2006).

Results of the study indicated both spatial and temporal variation in soil available nitrate, while ammonium and phosphate principally demonstrated temporal variations. Spatial trends indicated higher nitrate concentration in lower topographic zones, which further increased with reflooding, indicating that flood cessation was a major factor accounting for lower nitrate concentration at the end of implementation of flooding treatments. This suggests that plants in lower topographic zones of flood cessation wetlands are nutrophiles, and increased in diversity, richness and relative abundance by actively taking up soil available nitrate for rapid growth, a critical process in phyto-remediation (Doub 2000). However, the increased nitrate concentration following reflooding occurred likely because reflooding led to greater mortality, decay and decomposition of vegetation that re-colonized the previously dried wetlands, and facilitated release of nutrients from dead plant tissues to accumulate in the soils.

In contrast, soil available ammonium indicated strong flooding treatment effects, with greater levels on SF and flood cessation wetlands but least on FF wetlands in both 2003 and 2004. Only SF wetlands had the least level of ammonium with reflooding in 2005. The mechanism behind ammonium dynamics is unclear and it is suspected to be the result of interplaying effects of soil moisture and the biophysical processes involved in soil nitrogen conversion from ammonium to nitrate, and vice versa (Mitsch and Gosselink 2000).

Soil available phosphate levels increased with flood cessation from 2003 to 2004 but subsequently decreased with reflooding in 2005. Temporal trend in phosphate dynamics was in contrast to that of nitrate. Increased accumulation (loading) of phosphorus occurred in 2004 likely because of lack of abundant *T. latifolia* to actively take up the nutrient as a result of flood cessation. *T. latifolia* recovery with reflooding probably led to increased phosphorus uptake in 2005, and hence the subsequent reduction in phosphate levels (Weng et al. 2006).

The relative abundance of individual plant species varied in response to the presence and absence of cattle grazing across topographic positions of flood cessation wetlands. For example, grazed areas had greater abundance of *A. smithii, C. filifolia, A. pectiniforme, E. glandulosum, H. jubatum, P. palustris* and *C. arvense* but reduction in the relative abundance of *S. comata, P. pratensis* and *S. arvensis*. A notable observation is that cattle grazing impacted plant species in lower topographic zones of flood cessation wetlands. In particular, grazed areas had greater abundance of wetland plants *Rumex occidentalis*, but less of *E. palustris* and *T. latifolia*. Species that increased under cattle grazing are mostly unpalatable forage. On the other hand, forage species such as *S. comata, P. pratensis, E. palustris* and *S. arvensis* are very palatable to cattle, and hence experienced significant reduction in relative abundance under cattle grazing (Walker and Coupland 1970). Although it is not a highly preferred forage, cattle grazing appeared to cause significant reduction in the relative abundance of *T. latifolia*, and may thus hold promise for use as effective control method alongside to flood cessation.

4.5. Conclusions and Management Implications

The present study revealed that artificial flooding and flood cessation are important factors that may affect plant community succession in created wetlands of the

Dry Mixed Grass Prairie. Artificial flooding during initial wetland development led to a reduction in native species diversity and simpler plant communities in lower topographic zones, including domination by *E. palustris*. Although upland communities subject to sub-irrigation remained more complex, species compositional changes were evident there as well. Invasion by introduced plants during initial wetland development at Contra-Costa were minimal, but included the appearance of *T. latifolia*, which began to occupy enhanced wetlands within two years of initial development. In addition to increases in the amount and seasonal availability of water, plant community changes are likely the result of altered nutrient cycling under flooding, including nitrogen and phosphorus mineralization and use. Within newly created wetlands, the use of management strategies that periodically reduce wetland permanence may help prevent extended anoxic conditions that lead to phosphorus loading and the invasion of undesirable plant species such as *T. latifolia*.

Fall and spring flooding of established wetlands at Kitsim produced similar effects on plant community dynamics, and neither of the two treatments was capable of controlling *T. latifolia* in affected wetlands. Among the flooding treatments investigated here, only the 2 years of flood cessation was capable of reducing *T. latifolia* abundance, and increased the diversity and richness of both native and introduced species. However, changes in *T. latifolia* community, even with 2 years of drying, was not able to restore the desired community dominated by *E. palustris*, even with the presence of cattle grazing, which reduced the relative abundance and vigor of *T. latifolia* that remained.

Although this study was conducted under stochastic environmental conditions, including above-normal precipitation from 2003 to 2005, the present results confirmed that of the tightly controlled greenhouse experiment reported in Chapter 3. Both experiments indicated that *T. latifolia* is very resistant to soil moisture stress, particularly in comparison to *E. palustris*. While *T. latifolia* appears to be difficult to control using short-term moisture stress, affected plant communities showed little sign of reverting to *E. palustris*. Overall, these results suggest the shift from undesirable to desirable communities may be difficult to achieve, and may require drying treatments much longer than 2 years in duration. In addition, long term precipitation data can be modeled to predict likelihood of natural drought condition in the Dry Mixed Grass Prairie, and incorporate this into anthropogenic flood cessation strategies to control *T. latifolia*.

Given these findings, it appears that the maintenance of desirable wetland plant communities should be a priority immediately after initiating flooding to develop wetlands in the Dry Mixed Grass Prairie, as there is greater likelihood of achieving this goal using floodwater manipulation practices early in the wetland development project. Moreover, close regulation of wetland flooding may be able to more closely emulate the ephemeral, seasonal flooding that NF basins in the Dry Mixed Grass Prairie are adapted to. For example, artificial flooding could be alternated with natural flooding to maintain desirable wetland plant communities, with flooding increased during dryer periods and reduced during periods of above-normal rainfall and potential *T. latifolia* expansion. This management approach may prevent the wetland plant community from undergoing advanced undesirable succession.

Table 4.1: Summary of statistical tests indicating *P*-values on the effects of flooding treatment, period of sampling, and depth of flooding (topographic position), during repeated annual sampling of volumetric soil moisture at Contra-Costa and Kitsim in May, July and August of 2003, 2004 and 2005.

Location	Sampling Year		
Treatment Effect	2003	2004	2005
		P-values	
Contra-Costa			
Flooding Treatment	0.08	0.10	0.06
Topographic Position	**<0.0001**	**<0.0001**	**<0.0001**
Flooding x Position	**<0.0001**	**<0.0001**	**<0.0001**
Period of Sampling	**<0.0001**	**<0.0001**	**<0.0001**
Period x Flooding	**0.005**	0.6	0.07
Period x Position	**<0.0001**	**<0.0001**	**<0.0001**
Period x Flooding x Position	**0.002**	**0.04**	**0.05**
Kitsim			
Flooding Treatment	**0.04**	**0.01**	0.17
Topographic Position	**<0.0001**	**<0.0001**	**<0.0001**
Flooding x Position	**0.002**	**<0.0001**	0.22
Period of Sampling	**<0.0001**	**<0.0001**	**<0.0001**
Period x Flooding	**<0.0001**	**0.001**	**<0.0001**
Period x Position	**<0.0001**	**<0.0001**	**<0.0001**
Period x Flooding x Position	**0.04**	**0.004**	**0.002**

Table 4.2: Spatial and temporal dynamics of volumetric soil moisture (%) across landscapes associated with newly created wetlands at Contra-Costa. Within a column, individual flooding treatment × topographic position means with different lowercase letters differ ($P < 0.05$). Within a sampling year, grand means of topographic position × sampling period interaction values with different uppercase letters differ ($P < 0.05$).

	Sampling Year						
Topogr. Position	2003		2004			2005	
Flooding Treat.	Early July	Mid August	Early May	Early July	Mid August	Early July	Mid August
	------------------------Volumetric Soil Moisture (%)------------------------						
Upland							
Natural Flooding	7.3 d	2.6 d	25.0 d	11.1 f	7.5 f	28.7 d	13.4 f
Fall Flooding	26.3 c	7.2 cd	37.8 cd	34.3 d	24.5 de	38.0 d	20.8 e
Spring Flooding	7.1 d	2.9 d	32.0 cd	12.9 f	13.4 ef	28.9 d	13.6 f
Mean	***13.6 C***	***4.2 D***	***30.8 C***	***19.4 CD***	***15.1 D***	***31.9 C***	***15.9 D***
(SE)	***(5.2)***	***(1.2)***	***(2.5)***	***(6.1)***	***(4.1)***	***(2.5)***	***(2.0)***
Waterline							
Natural Flooding	11.0 d	5.8 cd	44.0 c	19.3 ef	15.7 e	34.0 d	19.9 e
Fall Flooding	39.2 bc	21.6 b	61.6 bc	27.7 de	38.9 cd	45.5 cd	35.5 cd
Spring Flooding	40.3 bc	6.4 cd	100 a	44.4 c	37.9 cd	55.7 c	35.1 cd
Mean	***29.6 B***	***11.3 C***	***68.2 B***	***29.7 C***	***30.8 C***	***45.7 B***	***30.2 CD***
(SE)	***(7.6)***	***(4.2)***	***(13.6)***	***(6.2)***	***(6.2)***	***(5.2)***	***(4.2)***
Shallow Flooding							
Natural Flooding	35.8 bc	3.7 cd	72.5 b	46.1 c	17.8 e	74.3 bc	16.6 ef
Fall Flooding	78.4 a	40.3 a	100 a	76.7 b	49.7 c	81.5 ab	41.0 c
Spring Flooding	100 a	9.8 c	100 a	100 a	69.4 b	100 a	62.0 b
Mean	***70.1 A***	***17.3 C***	***90.5 A***	***74.0 AB***	***43.0 C***	***86.9 A***	***38.8 BC***
(SE)	***(15.2)***	***(8.8)***	***(7.8)***	***(12.7)***	***(11.0)***	***(6.1)***	***(9.7)***
Deep Flooding							
Natural Flooding	53.6 b	11.3 c	100 a	55.7 bc	32.6 cd	100 a	29.7 de
Fall Flooding	100 a	40.8 a	100 a	100 a	70.4 b	100 a	50.0 b
Spring Flooding	100 a	45.3 a	100 a	100 a	100 a	100 a	100 a
Mean	***84.3 A***	***31.2 B***	***100 A***	***84.9 A***	***67.4 B***	***100 A***	***61.5 B***
(SE)	***(12.8)***	***(8.3)***	-	***(12.3)***	***(15.9)***	-	***(16.8)***

Table 4.3: Summary of statistical tests indicating *P*-values on the effects of flooding treatment, depth of flooding (topographic position), and sampling year on the concentration of soil available nitrate, ammonium and phosphate in landscapes associated with created wetlands at Contra-Costa and Kitsim from 2003 to 2005.

Study Location Treatment Effect	DF	Soil Nutrient Nitrate	 Ammonium	 Phosphate
			P-values	
Contra-Costa				
Pre-flooding (Covariate)	*1*	0.19	0.85	***0.04***
Flooding Treatment	2	0.19	0.75	0.23
Topographic Position	3	0.39	**0.01**	**0.02**
Flooding x Position	6	0.07	0.06	**0.01**
Sampling Year	2	**<0.0001**	**0.01**	**<0.0001**
Year x Flooding	4	**0.02**	0.38	0.86
Year x Position	6	0.15	0.25	**0.04**
Year x Flooding x Position	12	0.07	0.17	0.45
Kitsim				
Flooding Treatment	3	0.70	**0.003**	0.35
Topographic Position	3	**0.005**	0.33	0.17
Flooding x Position	9	0.34	**0.005**	0.19
Sampling Year	2	**<0.0001**	**<0.0001**	**0.001**
Year x Flooding	6	0.21	**0.0002**	0.84
Year x Position	6	**0.0001**	0.10	0.09
Year x Flooding x Position	18	0.75	**0.0003**	0.94

Table 4.4a: Spatial variation in the mean concentration (ppm) of soil available nitrate, ammonium and phosphate in response to fall, spring and natural flooding treatments on newly created wetlands at Contra-Costa. Within a nutrient, means of flooding treatment × topographic position interaction with different lowercase letters differ ($P < 0.05$). Grand (position) means with different uppercase letters differ ($P < 0.05$).

Nutrient Type	Topographic Position			
Flooding Treatment	Upland	Waterline	Shallow Zone	Deep Zone
	----Concentration (ppm)----			
Nitrate				
Fall Flooding	10.9	6.0	8.7	7.7
Spring Flooding	5.1	10.3	8.3	5.4
Natural Flooding	4.0	9.4	4.6	5.1
Mean	***6.7***	***8.6***	***7.2***	***6.1***
(SE)	***(1.7)***	***(1.1)***	***(1.1)***	***(0.7)***
Ammonium				
Fall Flooding	5.4 d	7.4 cd	21.5 a	22.7 a
Spring Flooding	5.6 d	22.0 a	22.2 a	16.5 b
Natural Flooding	10.9 c	12.4 bc	13.6 bc	13.8 bc
Mean	***7.3 B***	***14.0 A***	***19.1 A***	***17.7 A***
(SE)	***(1.5)***	***(3.5)***	***(2.3)***	***(2.2)***
Phosphate				
Fall Flooding	13.8 c	11.1 cd	19.8 b	21.0 ab
Spring Flooding	8.8 d	19.0 b	14.1 c	17.1 b
Natural Flooding	16.0 bc	24.8 a	13.1 cd	26.4 a
Mean	***12.9 C***	***18.3 AB***	***15.7 BC***	***21.5 A***
(SE)	***(1.7)***	***(3.2)***	***(1.7)***	***(2.2)***

Table 4.4b: Annual variation in mean concentration (ppm) of soil available nitrate and phosphate in response to fall, spring and natural flooding treatments and across topographic positions on newly created wetlands at Contra-Costa. Within a nutrient type, interaction means with different lowercase letters differ ($P < 0.05$). Grand (sampling year) means with different uppercase letters differ ($P < 0.05$).

Nutrient Type	Sampling Year		
Flooding Treatment /Topographic position	2003	2004	2005
	-----Concentration (ppm)-------		
Nitrate			
Fall Flooding	5.5 cd	3.9 de	15.7 a
Spring Flooding	6.5 c	6.3 c	9.1 b
Natural Flooding	4.2 de	3.1 e	9.9 b
Mean	***5.4 B***	***4.4 B***	***11.6 A***
(SE)	***(0.5)***	***(0.8)***	***(1.7)***
Phosphate			
Upland	11.2 c	18.3 b	9.2 c
Waterline	12.3 c	21.2 b	21.5 b
Shallow Flooding	11.3 c	22.5 ab	13.1 c
Deep Flooding	11.6 c	26.9 a	25.9 a
Mean	***11.6 C***	***22.2 A***	***17.4 B***
(SE)	***(0.2)***	***(1.6)***	***(3.3)***

Table 4.5: Summary of statistical tests indicating *P*-values of the effects of flooding treatment, depth of flooding (topographic position), and sampling year on the diversity and richness of native and introduced species in landscapes associated with newly created wetlands at Contra-Costa.

Vegetational Group Treatment Effect	DF	Diversity	Richness
		------*P* values-------	
Native Species			
Covariate (Pre-flooding)	1	0.17	0.12
Flooding Treatment	2	0.15	0.14
Topographic Position	3	**0.0001**	**0.0001**
Flooding x Position	6	0.60	0.27
Sampling Year	2	**0.09**	**0.01**
Flooding x Year	4	0.24	0.64
Position x Year	6	0.94	0.68
Flooding x Position x Year	12	0.45	0.37
Introduced Species			
Covariate (Pre-flooding)	1	**0.03**	0.17
Flooding Treatment	2	0.57	0.40
Topographic Position	3	0.20	0.20
Flooding x Position	6	0.16	0.43
Sampling Year	2	**0.02**	**0.05**
Flooding x Year	4	0.78	0.93
Position x Year	6	0.44	0.23
Flooding x Position x Year	12	0.42	0.85

Table 4.6a: Spatial (i) and temporal (ii) variation in the diversity and richness of native species in landscapes associated with newly created wetlands at Contra-Costa. Within a variable, grand means of topographic position (i) or sampling year (ii) with different uppercase letters differ ($P < 0.05$).

(i) Topographic Position Effect

Flooding Treatment	Native Species Diversity				Native Species Richness			
	Upland	Waterline	Shallow Zone	Deep Zone	Upland	Waterline	Shallow Zone	Deep Zone
	Shannon Index (H)				No. Species /2 m^2			
Fall Flooding	1.6	0.8	0.5	0.1	9.6	5.8	3.4	1.3
Spring Flooding	1.7	1.2	0.6	0.2	9.6	6.2	3.1	1.5
Natural Flooding	1.4	1.3	1.3	0.4	8.5	7.2	9.1	2.8
Mean	***1.5 A***	***1.1 AB***	***0.8 B***	***0.2 C***	***9.2 A***	***6.4 B***	***5.2 B***	***1.9 C***
(SE)	***(0.05)***	***(0.12)***	***(0.20)***	***(0.06)***	***(0.31)***	***(0.32)***	***(1.59)***	***(0.37)***

(ii) Sampling Year Effect

Flooding Treatment	Native Species Diversity			Native Species Richness		
	2003	2004	2005	2003	2004	2005
	Shannon Index (H)			No. Species /2 m^2		
Fall Flooding	0.8	0.7	0.8	5.3	4.0	5.9
Spring Flooding	1.1	0.7	0.9	5.9	4.4	5.0
Natural Flooding	1.0	1.1	1.1	6.9	6.1	7.6
Mean	***1.0 A***	***0.8 B***	***0.9 AB***	***6.0 A***	***4.8 B***	***6.2 A***
(SE)	***(0.09)***	***(0.11)***	***(0.08)***	***(0.40)***	***(0.53)***	***(0.61)***

Table 4.6b: Temporal variation in the diversity and richness of introduced species in landscapes associated with newly created wetlands at Contra-Costa. Within a variable, grand means of sampling years with different uppercase letters differ ($P < 0.05$).

Flooding Treatment	**Introduced Species Diversity**			**Introduced Species Richness**		
	2003	2004	2005	2003	2004	2005
	-------Shannon Index (H) ---------			---------No. Species /2 m^2 -------		
Fall Flooding	0.03	0.02	0.05	0.3	0.2	0.3
Spring Flooding	0.02	0.03	0.09	0.4	0.3	0.7
Natural Flooding	0.02	0.01	0.05	0.4	0.3	0.6
Mean	***0.02 B***	***0.02 B***	***0.06 A***	***0.4 B***	***0.2 C***	***0.6 A***
(SE)	***(0.002)***	***(0.005)***	***(0.011)***	***(0.04)***	***(0.04)***	***(0.09)***

Table 4.7a: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in upland zones following artificial flooding of newly created wetlands at Contra-Costa during pre-flooding (2002) and end-of-flooding (2005) sampling.

Upland Zone at Contra-Costa

Scientific Name	Pre-Flooding (2002)			End-of-Flooding (2005)*		
	Natural	Fall	Spring	Natural	Fall	Spring
	Canopy Cover (%)					
Native Species						
Achillea millefolium	0	0.3	0	0	0.6	0.5
Agropyron smithii	7.2	13.1	5.5	27.9 a	8.8 c	18.0 b
Agropyron trachycaulum	0	1.2	0	0	2.4	0
Agrostis scabra	0	0	0	1.7 b	0 b	14.7 a
Antennaria parvifolia	0	1.2	0	0	0	0
Artemisia cana	10	0.6	0.6	0	0	0
Artemisia frigida	2.9	0	2.5	0	0	3.0
Artemisia ludoviciana	9.6	1.5	0	17	0	4.3
Atriplex nuttallii	0.7	0	2.9	0	4.4	0
Bouteloua gracilis	2.4	2.9	6.6	6.7 b	5.9 b	10.7 a
Carex atherodes	0	0	0	0	4.7	0
Carex filifolia	21.1	8.1	14.7	17.3 a	0 c	6.6 b
Carex utriculata	0	10	0	0 b	8.3 a	0 b
Deschampsia caespitosa	0	1.2	0	0	3.3	0
Eleocharis palustris	0	0	0	0	3.7	0
Epilobium glandulosum	0	0	0	0	0.6	0
Erigeron pumilus	0	1.5	0	0	0.6	0
Erysimum aspermum	0	0	0	0	0.3	0
Gaura coccinea	0	0	0	1.1	0	0
Grindelia squarrossa	0	1.5	0	0	0.3	0
Hordeum jubatum	0	3.9	0	0 c	6.6 a	2.5 b
Juncus balticus	0	3.3	0	0	2.7	0
Koeleria macrantha	0	3.5	0	2.2	0.3	0.5
Melilotus alba	0	2.1	0	0	0.3	0
Melilotus officinalis	0	0	0	0	0	0
Mentha arvensis	0	0	0	0	0.4	0
Opuntia polyacantha	0	3.2	0	2.2	1.2	0
Plantago elongata	0.5	0.3	7.8	0	0	1.0
Phlox hoodii	0	0	0	0	0	0
Poa palustris	0	0	0	0 b	6.5 a	0 b
Puccinellia nuttaliana	0	3.6	0	0	0	0
Ratibida columnifera	0	0.9	0	0	0	0
Rumex occidentalis	0	0	0	0	0.3	1.0

*End-of-Flooding canopy cover of *E. palustris*, *T. latifolia* and other species having at least 5% canopy coverage, with different lowercase letters differ ($P < 0.05$).

Table 4.7a (cont'd): Vegetation (native and introduced species) composition and relative abundance (canopy cover) in upland zones following artificial flooding of newly created wetlands at Contra-Costa during pre-flooding (2002) and end-of-flooding (2005) sampling.

Upland Zone at Contra-Costa						
Scientific Name	Pre-Flooding (2002)			End-of-Flooding (2005)*		
	Natural	Fall	Spring	Natural	Fall	Spring
	Canopy Cover (%)					
Native Species (cont'd)						
Selaginella densa	18.2	3.8	35.6	3.4 b	0.6 c	13.2 a
Solidago canadensis	2.4	4.4	0	0	0	0
Sphaeralcea coccinea	1.0	3.1	0	0.6 b	6.2 a	0 b
Stipa comata	8.1	2.9	0.6	3.6 c	11.5 a	6.6 b
Stipa viridula	0	0	0	3.4	0	0
Suaeda moquinii	0	0.3	6.9	0	0	0
Thermopsis rhombifolia	1.0	0	0	1.1	0	0
Introduced Species						
Cirsium arvense	0	4.1	0	0	0	0
Cirsium vulgare	0	0.6	0	3.4	0	0
Crepis tectorum	0	0	0	0	0	0.5
Medicago lupulina	0	0.3	0	0	0.3	0
Poa pratensis	0	1.2	0	0	3.8	0
Sonchus arvensis	0	0	0	0	4.4	0.5
Taraxacum officinale	0	1.2	0	0.6	2.1	0.5

*End-of-Flooding canopy cover of *E. palustris*, *T. latifolia* and other species having at least 5% canopy coverage, with different lowercase letters differ ($P < 0.05$).

Table 4.7b: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in waterline zones following artificial flooding of newly created wetlands at Contra-Costa during pre-flooding (2002) and end-of-flooding (2005) sampling.

Waterline Zone at Contra-Costa						
Scientific Name	Pre-Flooding (2002)			End-of-Flooding (2005)*		
	Natural	Fall	Spring	Natural	Fall	Spring
	Canopy Cover (%)					
Native Species						
Achiellea millefolium	4.2	0	1.9	1.4	0.3	0
Agropyron smitthii	0	0.8	0	0 c	2.2 b	11.9 a
Agropyron trachycaulum	0	1.1	0	0	0	0
Agrostis scabra	0	0	0	14.8 a	11.8 ab	7.5 b
Artemisia cana	0	6.0	3.1	0	0	0
Artemisia frigida	24.2	5.5	3.4	0	2.4	0
Artemisia ludoviciana	11.9	0	0	3.2	0	0
Atriplex nuttallii	0	0.3	10.9	0	0	0
Beckmannia syzigachne	0	1.1	0	0	2.0	1.1
Carex atherodes	0	1.1	0	0	0	0
Carex filifolia	19.0	11.5	33.1	4.8	0	0
Carex utriculata	0	0.5	0	0	1.7	0
Eleocharis palustris	0	16.4	0	0 c	40.0 a	16.2 b
Epilobium glandulosum	0	0	0	0	0.3	0
Erigeron pumilus	0	0	0	0	0.3	0
Hordeum jubatum	0	11.5	0	0.5 c	2.7 b	5.4 a
Juncus balticus	0	7.7	0	0	2.4	0
Koeleria macrantha	0	0.5	0	0	0	0
Mentha arvensis	17.8	0	20.1	32.5 a	23.3 b	36.4 a
Orthocarpus luteus	0	0.3	0	0	0.6	0
Penstemon procerus	2.0	0	0	0	0	0
Plantago elongata	0	0	0.6	0.6	0	0
Poa palustris	0	0	0	16.8 a	1.5 c	4.3 b
Polygonum amphibium	0	0	0	2.6	0.6	0
Puccinellia nuttaliana	1.0	0	0	3.6	0	0
Rumex occidentalis	0	0	0	0	0.6	1.1
Scirpus pungens	0	0	0	0	1.8	0
Selaginella densa	0	9.8	0.6	0	0	0
Solidago canadensis	1.5	2.3	0	0	0	0
Stipa comata	0.5	5.2	0	0	0	0
Suaeda moquinii	0	0	2.5	0	0	0

*End-of-Flooding canopy cover of *E. palustris*, *T. latifolia* and other species having at least 5% canopy coverage, with different lowercase letters differ ($P < 0.05$).

Table 4.7b (cont'd): Vegetation (native and introduced species) composition and relative abundance (canopy cover) in waterline zones following artificial flooding of newly created wetlands at Contra-Costa during pre-flooding (2002) and end-of-flooding (2005) sampling.

Waterline Zone at Contra-Costa						
Scientific Name	Pre-Flooding (2002)			End-of-Flooding (2005)*		
	Natural	Fall	Spring	Natural	Fall	Spring
	Canopy Cover (%)					
Introduced Species						
Chenopodium album	0	0	0	0	0.3	0
Cirsium arvense	0	3.0	0	0	0	0
Medicago lupulina	0	0.4	0	0	0	0
Poa pratensis	0	3.0	0	0	0.3	0
Potentilla norvegica	1.0	0.3	0	1.2	0	0
Sonchus arvensis	0	0	0	0	0.6	0
Taraxacum officinale	0	0.8	0	1.1	0.3	1.1
Tragopogon dubius	0	0	0	0.6	0	0

*End-of-Flooding canopy cover of *E. palustris*, *T. latifolia* and other species having at least 5% canopy coverage, with different lowercase letters differ ($P < 0.05$).

Table 4.7c: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in shallow flooding zones following artificial flooding of newly created wetlands at Contra-Costa during pre-flooding (2002) and end-of-flooding (2005) sampling.

Shallow Flooding Zone						
Scientific Name	Pre-Flooding (2002)			End-of-Flooding (2005)*		
	Natural	Fall	Spring	Natural	Fall	Spring
	Canopy Cover (%)					
Native Species						
Agropyron smithii	35.9	19.4	51.6	31.9 a	0 b	0 b
Agrostis scabra	0	0	0	1.5 b	7.0 a	0 b
Alopecurus aequalis	0	0	0	0.7 b	0.8 b	16.4 a
Artemisia cana	0	3.9	0	0	0	0
Artemisia frigida	10.8	0	11.3	0	0	0
Artemisia ludoviciana	1.4	0	0	0.4	0	0
Atriplex nuttallii	0.5	1.1	5.6	0	0	0
Beckmannia syzigachne	0	1.2	0	9.4 a	0.8 b	0.5 b
Carex filifolia	0.9	10.9	5.0	0	0	0
Carex utriculata	0	0	0	0	0.3	0
Deschampsia caespitosa	0	0	0	2.2	0.6	0
Eleocharis palustris	16.3	26.9	0	19.2 b	67.2 a	74.4 a
Gaura coccinea	0	0.9	0	0	0	0
Hordeum jubatum	3.6	17.6	0.6	3.7	3.4	0
Melilotus officinale	0	0	0.6	0	0	0
Mentha arvensis	0	0	0	5.7 a	0 b	0 b
Poa palustris	0	0	0	12.7 a	0.3 b	0 b
Polygonum amphibium	0	0	0	0.4	4.5	0
Rumex occidentalis	0.5	0	0.6	1.1	2.2	0
Solidago canadensis	0	0.6	0	0	0	0
Introduced Species						
Chenopodium album	0	10.1	0	0	0	0
Medicago lupulina	0	0.6	0	0	0	0
Taraxacum officinale	0	0	0	0.4	0	0
Typha latifolia	0	0	0	0 c	2.4 b	8.7 a

*End-of-Flooding canopy cover of *E. palustris*, *T. latifolia* and other species having at least 5% canopy coverage, with different lowercase letters differ ($P < 0.05$).

Table 4.7d: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in deep flooding zones following artificial flooding of newly created wetlands at Contra-Costa during pre-flooding (2002) and end-of-flooding (2005) sampling.

Deep Flooding Zone						
Scientific Name	Pre-Flooding (2002)			End-of-Flooding (2005)*		
	Natural	Fall	Spring	Natural	Fall	Spring
	Canopy Cover (%)					
Native Species						
Achillea millefolium	5.4	0	0	0	0	0
Agropyron smithii	1.1	0	1.3	0	0	0
Alopecurus aequalis	0	1.7	0	2.7	0	0
Atriplex nuttallii	4.1	3.0	13.5	0	0	0
Beckmannia syzigachne	0.5	0	0	15.0 a	0 b	0 b
Bouteloua gracilis	0	0	0	0	0	0
Eleocharis palustris	29.4	7.0	16.9	71.6 b	100 a	97.5 a
Gaura coccinea	0	0.7	0	0	0	0
Hordeum jubatum	13.9	26.3	11.9	3.2	0	0
Mentha arvensis	0.5	0	0	0	0	0
Polygonum amphibium	0	0	4.1	0	0	2.5
Rumex occidentalis	10.4	5.2	11.3	3.2	0	0
Senecio sp.	0.5	0	1.9	0	0	0
Introduced Species						
Chenopodium album	3.3	26.5	5.6	0	0	0
Cirsium arvense	3.8	0.3	0	0	0	0
Phleum pratense	0	0	0.6	0	0	0
Typha latifolia	0	0	0	4.3 a	0 b	0 b

*End-of-Flooding canopy cover of *E. palustris*, *T. latifolia* and other species having at least 5% canopy coverage, with different lowercase letters differ ($P < 0.05$).

Table 4.8: Spatial and temporal variation in volumetric soil moisture (%) within landscapes associated with established wetlands at Kitsim. Within a column, flooding treatment × topographic position means with different lowercase letters differ ($P < 0.05$). Within a sampling year, grand means of topographic position × period of sampling interaction with different uppercase letters differ ($P < 0.05$).

	Sampling Year and Month						
Topogr. Position	2003		2004			2005[2]	
Flooding Treat[1]	Early July	Mid August	Early May	Early July	Mid August	Early July	Mid August
	Volumetric Soil Moisture (%)						
Upland Zone							
Fall	16.8 d	13.9 cd	27.1 de	11.8 f	8.8 d	22.5 d	23.5 cd
Spring	11.8 de	3.9 e	24.2 e	10.2 f	8.0 d	18.1 e	18.1 d
1YNF	6.3 e	3.6 e	25.0 e	11.0 f	9.8 d	16.0 e	21.8 cd
2YNF	7.0 e	4.9 e	22.5 e	7.2 f	7.1 d	12.5 e	18.3 d
Mean	***11.1 D***	***7.2 D***	***24.7 C***	***10.1 D***	***8.4 D***	***17.3 D***	***20.4 D***
(SE)	***(2.1)***	***(2.1)***	***(0.8)***	***(0.9)***	***(0.5)***	***(1.8)***	***(1.2)***
Dry Meadow							
Fall	31.2 c	23.7 b	44.7 c	26.8 d	21.6 b	30.3 cd	32.4 bc
Spring	28.1 c	9.8 d	42.4 c	14.6 ef	17.7 c	40.8 c	26.6 c
1YNF	36.6 c	9.7 d	34.9 cd	11.5 f	12.0 c	32.6 cd	22.6 cd
2YNF	15.1 d	7.4 d	31.7 d	11.1 f	9.8 d	23.2 d	22.8 cd
Mean	***27.9 C***	***12.8 D***	***38.4 B***	***16.0 D***	***15.3 D***	***31.7 C***	***26.1 CD***
(SE)	***(4.0)***	***(3.2)***	***(2.7)***	***(3.2)***	***(2.3)***	***(3.1)***	***(2.0)***
Wet Meadow							
Fall	46.4 b	25.3 ab	51.4 bc	42.4 bc	24.7 b	57.7 b	37.8 b
Spring	50.7 b	8.7 d	59.0 b	32.2 cd	24.0 b	59.6 b	36.1 b
1YNF	49.0 b	15.4 c	44.4 c	16.4 e	14.5 c	60.5 b	33.4 bc
2YNF	30.7 c	10.2 d	34.7 cd	13.8 f	13.8 c	42.3 c	32.2 bc
Mean	***44.1 B***	***15.1 D***	***47.4 B***	***26.2 C***	***19.3CD***	***54.5 B***	***35.0 C***
(SE)	***(3.9)***	***(3.3)***	***(4.5)***	***(5.9)***	***(2.6)***	***(3.6)***	***(1.1)***
Deep Marsh							
Fall	62.5 a	23.7 b	100 a	61.2 a	37.3 a	100 a	42.9 ab
Spring	61.0 a	23.8 b	100 a	49.3 ab	34.4 a	100 a	49.1 a
1YNF	61.7 a	31.6 a	49.7 bc	26.2 d	23.1 b	64.0 b	35.9 b
2YNF	38.0 c	16.1 c	45.2 c	21.7 de	19.0 bc	47.9 bc	35.7 b
Mean	***55.0 A***	***24.0 C***	***73.7 A***	***39.6 B***	***28.5 C***	***77.0 A***	***39.6 C***
(SE)	***(4.8)***	***(2.8)***	***(13.2)***	***(8.1)***	***(3.8)***	***(11.7)***	***(3.4)***

[1] 1YNF and 2YNF treatments represent one year and two years of no flooding (flood cessation), respectively.

[2] Final year sampling in 2005 is indicative of soil moisture during the growing season following post treatment reflooding.

Table 4.9a: Spatial and temporal variation in the concentration (ppm) of soil available nitrate in landscapes associated with established wetlands at Kitsim. Interaction means with different lowercase letters differ ($P < 0.05$). Topographic position grand means with different uppercase letters differ ($P < 0.05$). Sampling year grand means with different uppercase letters differ ($P < 0.05$)

Topographic Position	Sampling Years			***Mean***	***(SE)***
	2003	2004	2005[1]	***(Position)***	
	Nitrate Concentration (ppm)				
Upland	4.9 d	2.7 d	8.9 bc	***5.5 B***	***(0.7)***
Dry Meadow	6.5 cd	3.3 d	4.4 cd	***4.7 B***	
Wet Meadow	7.8 c	3.8 d	10.7 ab	***7.4 A***	
Deep Marsh	5.5 d	4.0 d	12.7 a	***7.4 A***	
Mean (Year)	***6.2 B***	***3.5 C***	***9.2 A***		
(SE)		***(1.7)***			

[1] Final year sampling in 2005 is indicative of soil nitrate concentrations following post treatment reflooding.

Table 4.9b: Spatial and temporal variation in soil ammonium concentration (ppm) within landscapes associated with established wetlands at Kitsim. Within a sampling year, flooding treatment × topographic position means with different lowercase letters differ ($P < 0.05$). Within a sampling year, flooding treatment grand means with different uppercase letters differ ($P < 0.05$).

Flooding Treatment Topographic Position	Sampling Year		
	2003	2004	2005[2]
	—Ammonium Concentration (ppm)—		
Fall Flooding			
Upland	4.9 d	2.7 d	8.9 b
Dry Meadow	6.5 d	3.3 d	4.4 d
Wet meadow	7.8 d	3.8 cd	10.7 a
Deep Marsh	5.5 d	4.0 c	12.7 a
Mean	***6.2 C***	***3.5 C***	***9.2 A***
(SE)	***(0.6)***	***(0.3)***	***(1.8)***
Spring Flooding			
Upland	9.0 c	5.4 c	8.6 b
Dry Meadow	8.1 cd	6.1 bc	6.5 d
Wet meadow	16.8 b	6.1 bc	5.7 d
Deep Marsh	7.7 d	6.5 b	6.5 d
Mean	***10.4 AB***	***6.0 B***	***6.8 B***
(SE)	***(2.2)***	***(0.2)***	***(0.6)***
1YNF			
Upland	11.0 c	4.5 c	9.0 b
Dry Meadow	15.3 b	6.8 b	8.8 b
Wet meadow	14.1 b	9.1 a	7.5 c
Deep Marsh	23.4 a	7.8 ab	6.9 c
Mean	***16.0 A***	***7.1 A***	***8.1 AB***
(SE)	***(2.6)***	***(1.0)***	***(0.5)***
2YNF			
Upland	10.8 c	8.9 a	9.8 ab
Dry Meadow	8.5 cd	5.5 c	7.3 c
Wet meadow	8.1 cd	4.3 c	8.2 bc
Deep Marsh	6.1 d	10.5 a	8.3 bc
Mean	***8.4 BC***	***7.3 A***	***8.4 AB***
(SE)	***(1.0)***	***(1.4)***	***(0.5)***

[1] 1YNF and 2YNF treatments represent one year and two years of no flooding (flood cessation), respectively.

[2] Final year sampling in 2005 is indicative of soil ammonium concentration the growing season following post treatment reflooding.

Table 4.10: Summary of statistical tests indicating *P*-values on the effects of flooding treatment, presence of cattle grazing and topographic position, on the diversity and richness of native and introduced species at each of two sampling periods, including end-of-treatment (2004) and post-treatment reflooding (2005), in landscapes associated with older, established wetlands at Kitsim.

Vegetational Group		Diversity		Richness	
Treatment Effect	DF	End[1]	Post	End	Post
		----------------------	*P*-value	----------------------	
Native Species					
Covariate (Pre-flooding)	1	**<0.0001**	0.31	**<0.0001**	**<0.0001**
Flooding Treatment	3	0.20	0.21	0.20	**0.01**
Grazing	1	**0.04**	0.33	**0.04**	0.65
Flooding x Grazing	3	0.80	0.32	0.80	0.87
Position	3	**0.02**	0.48	**0.02**	**<0.0001**
Flooding x Position	9	0.12	0.43	0.12	**0.03**
Grazing x Position	3	0.60	0.40	0.60	0.65
Flooding x Grazing x Position	9	0.56	0.42	0.56	0.99
Introduced Species					
Covariate (Pre-flooding)	1	**<0.0001**	**<0.0001**	**0.0002**	**<0.0001**
Flooding Treatment	3	**0.09**	**0.05**	**0.01**	**0.003**
Grazing	1	0.51	0.88	0.90	0.69
Flooding x Grazing	3	0.88	0.71	0.71	0.70
Position	3	**0.002**	**<0.0001**	**<0.0001**	**<0.0001**
Flooding x Position	9	0.10	**0.03**	0.10	0.48
Grazing x Position	3	0.58	0.41	0.20	0.33
Flooding x Grazing x Position	9	0.90	0.92	0.89	0.98

[1] End and Post represent end-of-treatment and post-treatment reflooding sampling periods.

Table 4.11a: Variation in native species diversity and richness during end-of-treatment (2004) and post-treatment reflooding (2005) sampling on landscapes associated with established wetlands at Kitsim. Within a response variable (species diversity or richness) and sampling period, topographic position × flooding treatment means with different lowercase letters differ ($P < 0.05$); topographic position grand means with different uppercase letters differ ($P < 0.05$); and flooding treatment grand means with different uppercase letters differ ($P < 0.05$). Numbers in parentheses are pooled standard errors of the associated grand means.

Sampling Period Flooding Treatment[1]	Native Species Diversity				Native Species Richness					
	Upland	Dry Meadow	Wet Meadow	Deep Marsh	Upland	Dry Meadow	Wet Meadow	Deep Marsh	***Mean Flooding***	***(SE)***
	Shannon Index (H)				No. Species /2 m^2					
End-of-Treatment										
Fall Flooding	1.2	1.1	1.3	0.8	6.7	7.4	6.3	4.4	***6.2***	
Spring Flooding	1.2	1.0	1.3	0.8	8.0	6.6	8.6	5.1	***7.1***	***(0.38)***
1YNF	1.3	1.2	1.2	1.3	9.8	7.5	7.6	7.2	***8.0***	
2YNF	1.3	1.0	1.2	1.2	7.9	6.4	7.5	7.8	***7.4***	
Mean (Position)	***1.3A***	***1.1AB***	***1.2AB***	***1.0B***	***8.1 A***	***7.0 AB***	***7.5 A***	***6.1 B***		
(SE)		***(0.06)***				***(0.41)***				
Post-Treatment Re-flooding										
Fall Flooding	1.1	1.1	1.2	0.9	6.2 bc	8.7 ab	7.0 b	3.7 d	***6.9 B***	
Spring Flooding	1.2	0.9	1.3	0.5	8.6 ab	7.7 b	8.4 ab	3.0 d	***8.1 A***	***(0.25)***
1YNF	1.3	1.4	1.5	1.0	10.7 a	8.1 ab	8.8 ab	4.7 cd	***7.5 AB***	
2YNF	1.2	1.1	1.4	1.2	8.3 ab	7.9 b	8.1 ab	5.9 c	***7.2 B***	
Mean (Position)	***1.2***	***1.1***	***1.3***	***0.9***	***8.4 A***	***8.1 A***	***8.1 A***	***4.3 B***		
(SE)		***(0.20)***				***(0.97)***				

[1] The 1YNF and 2YNF flooding treatments represent one year and two years of no flooding (flood cessation), respectively.

Table 4.11b: Variation in introduced species diversity and richness during end-of-treatment (2004) and post-treatment reflooding (2005) sampling on landscapes associated with established wetlands at Kitsim. Within a response variable (species diversity and richness) and sampling period, flooding treatment × topographic position means with different lowercase letters differ ($P < 0.05$); topographic position grand means with different uppercase letters differ ($P < 0.05$); flooding treatment grand means with different lowercase letters differ ($P < 0.05$). Numbers in parentheses are pooled standard errors of the associated grand means.

Sampling Period	Introduced Species Diversity						Introduced Species Richness					
Flooding Treatment[1]	Upland	Dry Meadow	Wet Meadow	Deep Marsh	***Mean (Flood)***	***(SE)***	Upland	Dry Meadow	Wet Meadow	Deep Marsh	***Mean (Flood)***	***(SE)***
	Shannon Index (H)						No. Species /2 m^2					
End-of-Treatment												
Fall Flooding	0.1	0.3	0.4	0.1	***0.2 C***	***(0.03)***	0.5	1.6	1.2	1.0	***1.1 B***	***(0.14)***
Spring Flooding	0.2	0.5	0.4	0.3	***0.3 B***		1.0	2.2	2.5	1.2	***1.7 A***	
1YNF	0.2	0.3	0.4	0.5	***0.3 B***		0.6	1.6	2.0	2.0	***1.5 A***	
2YNF	0.2	0.4	0.3	0.5	***0.4 A***		0.7	1.9	2.0	2.2	***1.7 A***	
Mean (Position)	***0.2B***	***0.4 A***	***0.4 A***	***0.3 AB***			***0.7 B***	***1.8 A***	***1.9 A***	***1.6 A***		
(SE)		***(0.05)***							***(0.28)***			
Post-Treatment Re-flooding												
Fall Flooding	0.1 a	0.3 c	0.3 c	0.2 c	***0.2 B***	***(0.03)***	0.5	1.3	1.2	1.1	***1.0 B***	***(0.17)***
Spring Flooding	0.2 c	0.5 b	0.6 b	0.0 d	***0.3 A***		1.91	2.0	2.7	1.1	***1.7 A***	
1YNF	0.2 c	0.3	0.3 c	0.2 c	***0.3 A***		0.9	1.8	2.0	1.1	***1.5 A***	
2YNF	0.2 c	0.4 bc	0.3 c	0.3 c	***0.3 A***		1.3	2.3	2.4	1.1	***1.7 A***	
Mean (Position)	***0.2 B***	***0.4 A***	***0.4 A***	***0.1 B***			***0.9 B***	***1.8 A***	***2.1 A***	***1.1 B***		
(SE)		***(0.06)***							***(0.28)***			

[1] The 1YNF and 2YNF flooding treatments represent one year and two years of no flooding (flood cessation), respectively.

Table 4.12a: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of upland zones associated with two years of flood cessation in established wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Upland Zone associated with 2YNF[1] Wetlands at Kitsim						
Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre[2]	End	Post
	----------------Canopy Cover (%) ---------------					
Native Species						
Achillea millefolium	0.9	2.3	1.7	1.7	1.7	3.1
Agropyron pectiniforme	0.9	1.9	3.1	0	0.3	0
Agropyron smithii	27.2	14.2	25.8	43.6*	25.3*	42.3*
Agrostis scabra	0	0	0.2	0	0	0
Antennaria parvifolia	0	0.2	0	0.3	0.6	0.2
Artemisia cana	0.6	0	0	1.4	0	1.6
Artemisia frigida	13.1	1.9	5.2	6.7*	2.8	3.4
Artemisia ludoviciana	0.3	0.8	0	0.2	0	0
Atriplex nuttallii	3.3	0	0	1.3	0	0
Bouteloua gracilis	3.4	3.3	3.3	2.3	2.9	0.9
Carex filifolia	11.6	11.6	13.6	10.8	11.7	17.8*
Erysimum asperum	0	0	0.8	0	0	0
Grindelia squarrosa	0.5	0.2	0	0	0	0
Gutierrezia sarothrae	0	0	0	0.2	0	0.2
Hordeum jubatum	0.2	0	0	0.8	0	0.2
Koeleria macrantha	0	3.0	1.9	0	1.7	1.4
Phlox hoodii	0	0	0	0.3	0	0.3
Plantago purshii	0	0	0	0.2	0	0
Poa palustris	0	0.2	0	0	0	0
Poa sandbergii	0	0	0.2	0	0	0.8
Potentilla sp.	1.1	0	0	0	0	0
Selaginella densa	11.1	6.3	6.9	11.4	1.7*	2.5*
Solidago canadensis	0	0.2	0.2	0.3	0	0
Sphaeralcea coccinea	4.8	2.5	5.0	0.3	0.2	0.3*
Stipa comata	8.3	6.6	10.9	1.1*	0.5*	1.4*
Stipa viridula	2.2	0.3	2.0	0	0	3.0
Thermopsis rhombifolia	0.9	0.2	0.5	0.2	0	0
Introduced Species						
Cirsium arvense	0	0	0	0	0.6	0.8
Medicago lupulina	0.2	0	0	0.3	0	0
Poa pratensis	0.5	10.4	1.1	8.1*	10.1	1.7
Sonchus arvensis	0	0	0	0	0.5	0
Taraxacum officinale	0	0	0.8	0	0.2	0.5
Tragopogon dubius	0.2		0.5	0.2	0.2	0.3

[1] The 1YNF treatments represents one year of flood cessation.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Table 4.12b: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of dry meadow zones associated with two years of flood cessation in established wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Dry Meadow Zone of 2YNF[1] Wetlands at Kitsim

Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre[2]	End	Post
	Canopy Cover (%)					
Native Species						
Achillea millefolium	0.5	0.8	1.4	0	1.3	3.4
Agropyron smithii	7.2	1.6	1.9	3.6*	3.0	8.3*
Agropyron trachycaulum	0	0	0	0	0	0.3
Agrostis scabra	0	0	0	0	0	0.2
Beckmannia syzigachne	0	0	0	0.3	0	0
Carex atherodes	0.9	0.9	2.5	0.2	0.2	2.8
Carex filifolia	1.7	0.4	1.4	1.1	2.0	2.5
Carex rostrata	2.0	0	0	0.3	0.6	0
Deschampsia caespitosa	4.7	3.0	0.9	8.6*	3.1	0.8
Eleocharis palustris	0.9	0	0.9	1.4	0	0
Erigeron canadensis	0	0	0	0	0	0.2
Erigeron pumillus	1.1	0	0	0.6	0	0
Erysimum asperum	0	1.3	0.2	0	0	0
Gutierrezia sarothrae	0.8	0.2	0	0.2	0	0.2
Hordeum jubatum	36.7	8.3	7.0	36.1	5.6*	5.0
Mentha aevensis	0.2	0.3	0.3	0.8	0.2	0.2
Poa palustris	3.6	11.0	7.0	4.4	13.4	16.4*
Polygonum sp.	0	0	0.3	0	0	0
Potentilla sp.	0	0	0	0.3	0	0
Ratibida columnifera	1.4	4.7	2.7	0	0.2	0.8
Rumex occidentalis	9.1	3.4	2.2	12.8	0.2*	0
Stipa comata	0	0	0	0	0	0.2
Thermopsis rhombifolia	0	0	0	0.2	0	0
Introduced Species						
Chenopodium album	0.2	0.5	0	0	0	0
Cirsium arvense	0.6	7.8	5.2	6.6*	17.3*	15.2*
Cirsium vulgare	0	0	0.3	0	0	0
Crepis tectorum	0	0	0.6	0	0	0
Poa pratensis	17.8	17.3	21.7	10.3*	10.6*	10.9*
Sonchus arvensis	1.9	8.9	15.0	2.2	6.7	4.8*
Taraxacum officinale	5.3	2.2	6.9	9.1*	2.2	4.5*
Tragopogon dubius	0.2	0	1.6	0.2	0.8	1.4
Typha latifolia	1.1	0	0	0.6	0	0

[1] The 1YNF treatments represents one year of flood cessation.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Table 4.12c: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of wet meadow zones associated with two years of flood cessation in established wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Wet Meadow Zone of 2YNF[1] Wetlands at Kitsim						
Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre	End	Post
	------------------Canopy Cover (%)------------------					
Native Species						
Achillea millefolium	0	0	0	0	0.2	0.3
Agropyron smithii	0	0	0	0.3	0	0
Alopecurus aequalis	0	0	0.3	0	0	0
Artemisia frigida	0	0	0	0	0.2	0
Bechmannia syzigachne	0	0.2	0	0	0	0
Carex utriculata	2.2	1.9	2.7	1.1	1.4	0.6
Eleocharis palustris	3.6	2.0	1.9	5.5	1.9	11.4*
Epilobium glandulosum	0	1.3	4.2	0	0	1.4
Erigeron pumillus	0.5	0	0	0.6	0	0
Erysimum aspermum	0	2.8	0.3	0	1.7	0.3
Grindelia squarossa	0	0	0	0	0.2	0
Hordeum jubatum	4.8	6.9	7.5	9.7*	9.7*	14.2*
Mentha arvensis	0	0	0	1.3	0.9	0
Poa palustris	0	1.9	3.1	0	5.3*	8.9*
Polygonum amphibium	1.6	0	0.6	0.5	0	0.6
Potentilla fruticosa	0	0.3	0	0	0	0
Puccinellia nuttaliana	0	0	0	2.7	0	0
Rumex occidentalis	35.9	18.0	14.2	42.0*	5.8*	13.8
Scirpus pungens	1.3	0	1.4	2.5	0.3	1.6
Stipa viridula	1.1	0	0	0	0	0
Introduced Species						
Chenopodium album	0	0.2	1.6	0	0	0.6
Cirsium arvense	1.9	14.4	10.3	0.5	21.7*	7.5*
Lactuca sp.	0	0	8.6	0	0	0.8*
Poa pratensis	0	0.2	0.2	0	0.3	1.1
Potentilla norvegica	0	0	0	0.5	1.6	0.3
Senecio vulgaris	0	2.5	0	0	2.8	2.2
Sonchus arvensis	0.9	20.8	11.7	0	20.8	11.9
Taraxacum officinale	4.5	0	0.2	8.4	0	0.2
Tragopogon dubius	0	0	0.2	0	0	0
Typha latifolia	38.6	2.8	2.8	22.8*	1.4	4.5

[1] The 2YNF treatment represents two years of flood cessation.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Table 4.12d: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of deep marsh zones associated with two years of flood cessation in established wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Deep Marsh Zone of 2YNF[1] Wetlands at Kitsim						
Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre	End	Post
	Canopy Cover (%)					
Native Species						
Achillea millefolium	0	0.2	0	0	0	0
Beckmannia syzigachne	0	0.9	1.9	0	0	0.8
Eleocharis palustris	0.8	0.9	1.4	0.3	0	0
Epilobium glandulosum	0	0.9	2.2	0	1.6	0.3
Erysimum aspermum	0	3.0	0	0	2.8	0
Hordeum jubatum	1.4	1.7	6.1	0.6	1.6	8.9*
Poa palustris	0	0	0.3	0	0	0
Polygonum amphibium	3.9	0.3	0.2	1.4	0.3	0
Rumex occidentalis	11.4	20.5	17.0	14.1	18.4	28.9*
Scirpus pungens	5.2	1.6	3.8	0	0	0
Senecio vulgaris	0	0.2	0	0	0.5	0
Introduced Species						
Chenopodium album	0	0.2	0.8	0	0.2	2.2
Cirsium arvense	0.2	3.6	0	0	3.1	1.9
Lactuca sp.	0	0	3.9	0	0	1.1
Sonchus arvensis	0	16.1	0.9	0	25.2*	0
Taraxacum officinale	2.0	0.2	0	5.0	0.2	0
Typha latifolia	68.0	11.3	19.5	77.7	6.9*	10.0*

[1] The 2YNF treatment represents two years of flood cessation.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Table 4.12e: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of upland zones associated with one year of flood cessation in established wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Upland Zone of 1YNF[1] Wetlands at Kitsim						
Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre[2]	End	Post
	Canopy Cover (%)					
Native Species						
Achillea millefolium	3.1	1.1	0.6	2.0	1.4	2.2
Agropyron pectiniforme	0.9	0.9	3.9	23.1*	21.4*	21.7*
Agropyron smithii	21.4	10.4	21.7	20.1	13.3*	19.7
Agropyron trachycaulum	0	0	0.2	0	0	0
Agrostis scabra	0.3	0.3	0.2	0	0	0
Antennaria parvifolia	0.9	1.3	0.6	0	0.3	0.2
Artemisia cana	0	0	0.9	0	0	0
Artemisia frigida	2.3	6.2	4.4	1.3	3.4*	9.7*
Artemisia ludoviciana	3.3	3.1	2.5	6.4*	1.3	0.6
Atriplex gardneri	0	0	0	0	0	0.6
Atriplex nuttallii	0	0.6	0.2	2.5	0.8	2.8
Bouteloua gracilis	0	0.2	1.4	0	0.2	3.7
Bromus inermis	1.3	0.8	0.6	0	0	0
Carex filifolia	19.8	12.6	7.8	19.5	10.3	12.2*
Deschampsia caespitosa	2.5	1.9	4.5	0	0	0
Distichlis spicta	1.9	1.3	0.9	0.3	1.7	0.2
Erigeron pumillus	0.2	0.2	0.3	0	0	0
Gutierrezia sarothrae	0.9	1.3	1.3	0.5	2.0	1.1
Hordeum jubatum	0.2	0.9	0.2	0	0	0
Koeleria macrantha	4.2	2.3	1.9	2.0	2.7	1.1
Phlox hoodii	1.4	0.8	0	0	0.5	0.2
Plantago purshii	0.2	0.2	1.1	0.6	0.2	0.2
Poa palustris	4.5	4.2	3.0	0	0	0
Potentilla sp.	0.2	0.2	0	0	0	0
Ratibida columnifera	0	1.0	0.3	0	0	0
Selaginella densa	11.1	4.6	6.9	4.8*	2.0	3.0*
Solidago canadensis	0.2	0	0.2	0	0	0
Sphaeralcea coccinea	0.2	0.3	0	1.1	0.9	0.5
Stipa comata	2.2	1.1	3.6	2.8	0.6	2.3
Stipa viridula	0	0	0	0.5	0	1.1
Thermopsis rhombifolia	0.8	0.3	0.3	0	0	0

[1] The 1YNF treatments represents one year of flood cessation.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Table 4.12e (cont'd): Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of upland zones associated with one year of flood cessation in established wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Upland Zone associated of 1YNF[1] Wetlands at Kitsim						
Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre[2]	End	Post
	----------------Canopy Cover (%) -------------					
Introduced Species						
Cirsium arvense	2.7	3.3	3.8	0	0	0.5
Poa pratensis	4.8	10.9	6.4	6.6	5.8*	2.0*
Taraxacum officinale	0	0.5	0.6	0	0	0
Tragopogon dubius	0	0	0	0	0.2	0.8

[1] The 1YNF treatments represents one year of flood cessation.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Table 4.12f: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of dry meadow zones associated with one year of flood cessation in established wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Dry Meadow Zone associated of 1YNF[1] Wetlands at Kitsim

Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre[2]	End	Post
	Canopy Cover (%)					
Native Species						
Achillea millefolium	0.3	0.2	0.2	1.1	1.1	0
Agropyron smithii	6.4	2.2	3.3	0.7*	0.6	1.6
Agropyron trachycaulum	0.3	0	0.5	0	0	0.2
Artemisia frigida	0	0	0	0	0.2	0.2
Artemisia ludoviciana	0	0.2	0	0	0	0
Beckmannia syzigachne	0.6	0	0.3	0.2	0	0
Carex filifolia	0	0.2	0	1.7	3.4	5.9*
Carex rostrata	15.8	11.1	15.1	15.2	9.5	9.7*
Carex sp.	0	0	0	0.2	0	0.3
Deschampsia caespitosa	2.7	1.6	2.5	0	0	0
Distichlis spicta	0.6	0.5	0	1.7	1.3	0
Eleocharis palustris	3.0	1.3	0.6	1.3	1.3	0
Erigeron canadensis	0	0	0.2	0	0	0
Erigeron pumillus	0	0	0	0	0	0.2
Gutierrezia sarothrae	0.2	0.9	0.3	0.2	0	0.2
Hordeum jubatum	1.3	2.5	3.1	2.3	1.9	5.8
Juncus balticus	0.2	0	0	1.3	0.2	0.2
Mentha aevensis	0.8	0.8	0.5	0.6	0.2	0.6
Poa palustris	11.7	8.3	13.8	14.1	10.2	15.0
Polygonum sp.	4.4	7.7	4.1	5.2	2.7*	5.0
Potentilla sp.	0	0	0	0	0.2	0.2
Ratibida columnifera	0.2	0.9	0.2	0.5	0.3	0.5
Rumex occidentalis	0.2	0.3	1.4	0.6	0.2	1.7
Solidago canadensis	0	0.9	1.1	0	0	0
Introduced Species						
Chenopodium album	0	0	0.2	0	0	0
Cirsium arvense	16.1	17.2	5.2	18.4	12.0*	7.5
Cirsium vulgare	0	0.2	0.3	0	0.3	0.2
Poa pratensis	0.2	2.2	10.8	2.3	8.3*	8.6
Sonchus arvensis	14.2	21.3	23.8	16.1	19.2	28.9*
Taraxacum officinale	0	0.2	0.5	1.6	0.2	1.9
Tragopogon dubius	0	0.2	0	0	0.3	0.5
Typha latifolia	0.3	0.2	0.2	0.2	0	0

[1] The 1YNF treatments represents one year of flood cessation.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Table 4.12g: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of wet meadow zones associated with one year of flood cessation in established wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Wet Meadow Zone of 1YNF[1] Wetlands at Kitsim						
Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre	End	Post
	Cover (%)					
Native Species						
Agropyron smitthii	0	0	0.6	0	0	0
Alopecurus aequalis	0.4	0.5	0.9	0.5	2.2	1.4
Beckmannia syzigachne	0.4	0.6	0.6	0.3	0.6	4.1
Carex utriculata	3.8	2.7	11.9	5.5	2.3	4.7*
Deschampsia caespitosa	0	1.9	1.1	2.0	0.5	1.3
Eleocharis palustris	29.7	28.6	23.9	30.3	21.3*	19.4
Epilobium glandulosum	0	2.3	0	0	0.3	0.3
Erigeron pumilus	0	0	0.2	0	0	0
Erysimum aspermum	0	0	0.2	0	0	0
Hordeum jubatum	1.3	4.5	2.7	0.3	2.5	10.2*
Juncus balticus	0	0	0	0.2	0	0
Mentha arvensis	1.3	0	0	7.3*	0	0.2
Poa palustris	0.6	0.8	6.9	0	3.0*	10.2*
Polygonum amphibium	8.2	3.9	5.3	11.6	3.9	4.2
Rumex occidentalis	9.1	13.0	10.3	2.2	9.7*	10.6
Scirpus pungens	2.5	0.9	0.2	0	0.2	0.3
Solidago Canadensis	0	0.2	0.2	0	0	0
Introduced Species						
Chenopodium album	0	0	0.9	0	0	0.8
Cirsium arvense	0	4.7	0.6	3.6	9.8*	2.2*
Lactuca sp.	0	0	0.2	0	0	1.4
Poa pratensis	0	0	0.2	0	0	2.0
Sonchus arvensis	1.3	4.2	4.1	1.3	2.0	7.2*
Taraxacum officinale	0.2	0	0	0	0	0.3
Typha latifolia	25.2	6.6	12.5	20.8*	6.6	9.1*

[1] The 1YNF treatments represent one year of flood cessation.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Table 4.12h: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of deep marsh zones associated with one year of flood cessation in established wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Deep Marsh Zone of 1YNF[1] Wetlands at Kitsim

Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre	End	Post
	Canopy Cover (%)					
Native Species						
Agropyron smithii	0	0	0	0	0	0.2
Alopecurus aequalis	0	0.2	0	1.3	0.9	0.6
Beckmannia syzigachne	0	0	0.2	0	0.2	0.2
Deschampsia caespotosa	0	0	0	0	0.2	0
Eleocharis palustris	37.5	19.4	35.8	12.1*	8.9*	37.5
Epilobium glandulosum	0	0.8	0	0	0.6	0
Erysimum aspermum	0	0.6	0	0	1.1	0
Hordeum jubatum	0	2.5	1.4	0	1.9	0.6
Juncus balticus	0	0	0	4.2	0	0
Polygonum amphibium	0	1.1	0.2	0	0.2	0.2
Rumex occidentalis	0	13.3	3.3	0	25.3*	5.1
Schizachne purpurascense	0	0	1.1	0	0	0
Scirpus pungens	3.8	0.2	0	0	0.2	1.6
Introduced Species						
Chnenopodium album	0	0.2	0	0	0	0
Cirsium arvense	0	0.3	0	0	1.3	0
Sonchus arvensis	0	1.9	35.8	0	1.3	0*
Typha latifolia	58.8	25.3	45.6	72.5*	19.7*	32.3*

[1] The 1YNF treatments represents one year of flood cessation.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

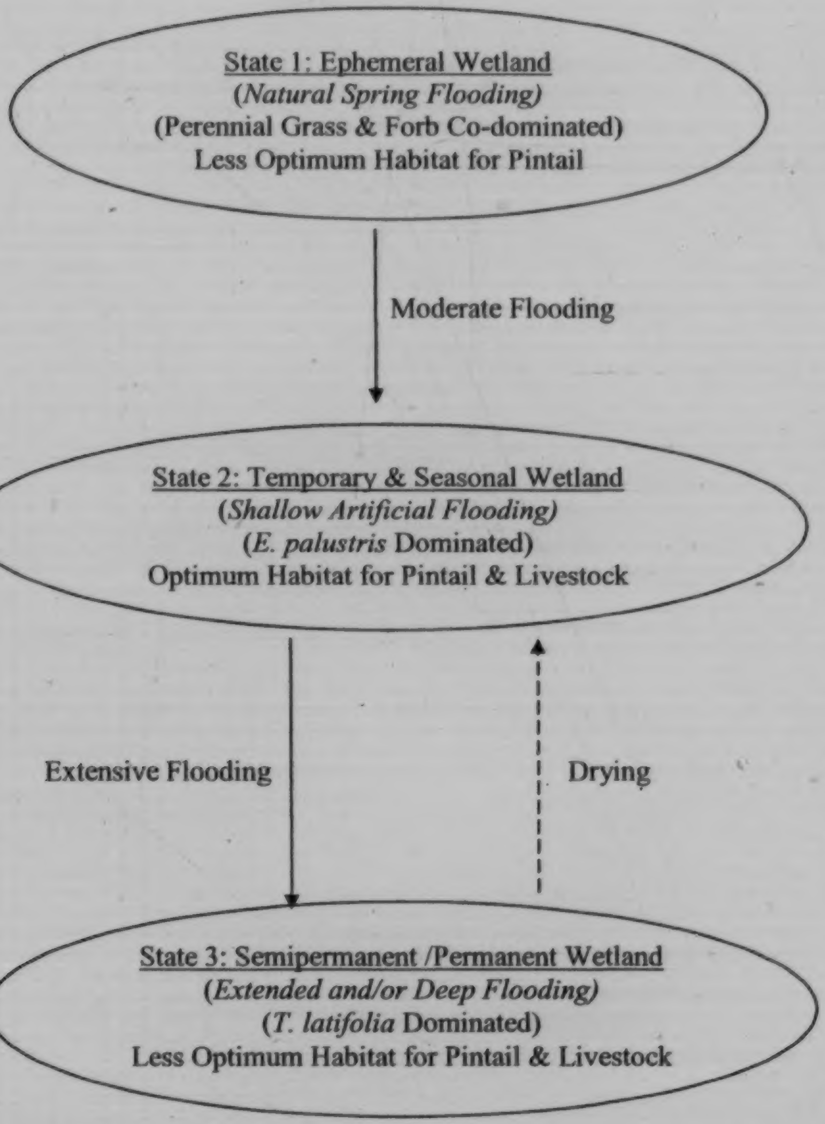
State 1: Ephemeral Wetland
(Natural Spring Flooding)
(Perennial Grass & Forb Co-dominated)
Less Optimum Habitat for Pintail
Moderate Flooding
State 2: Temporary & Seasonal Wetland
(Shallow Artificial Flooding)
(E. palustris Dominated)
Optimum Habitat for Pintail & Livestock
Extensive Flooding
Drying
State 3: Semipermanent /Permanent Wetland
(Extended and/or Deep Flooding)
(T. latifolia Dominated)
Less Optimum Habitat for Pintail & Livestock

Fig. 4.1: Theorized model of vegetation succession following wetland creation in the Dry Mixed Grass Prairie of southeastern Alberta, Canada. State 2 constitutes the desired plant community (DPC) that provides the habitat mosaic optimum for Northern Pintail and rangeland cattle. While moderate and extensive flooding of newly created wetlands may facilitate succession to states 2 and 3, respectively, wetland drying may facilitate community change from state 3 to 2 (the DPC).

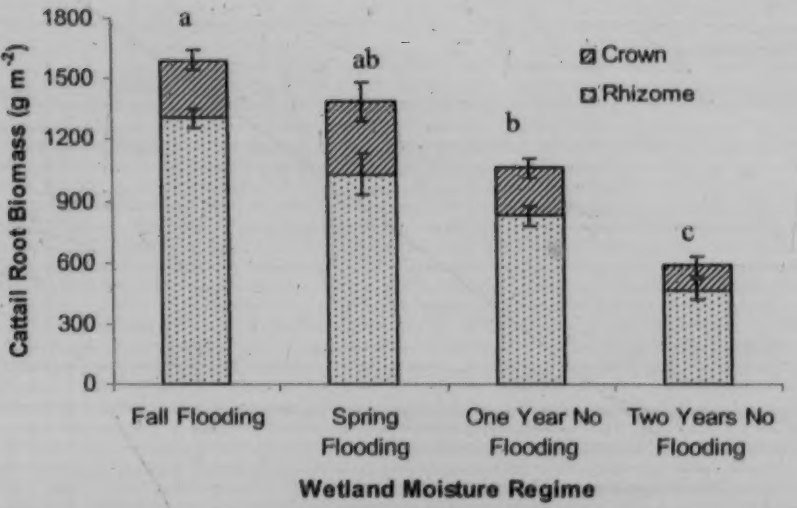

Fig. 4.2: Effects of four flooding treatments on mean (± SE) total *T. latifolia* root (crown and rhizome combined) biomass in established wetlands at Kitsim. Sampling was conducted in October 2005 after implementing post-treatment reflooding for one year. Column totals with different lowercase letters differ ($P < 0.05$).

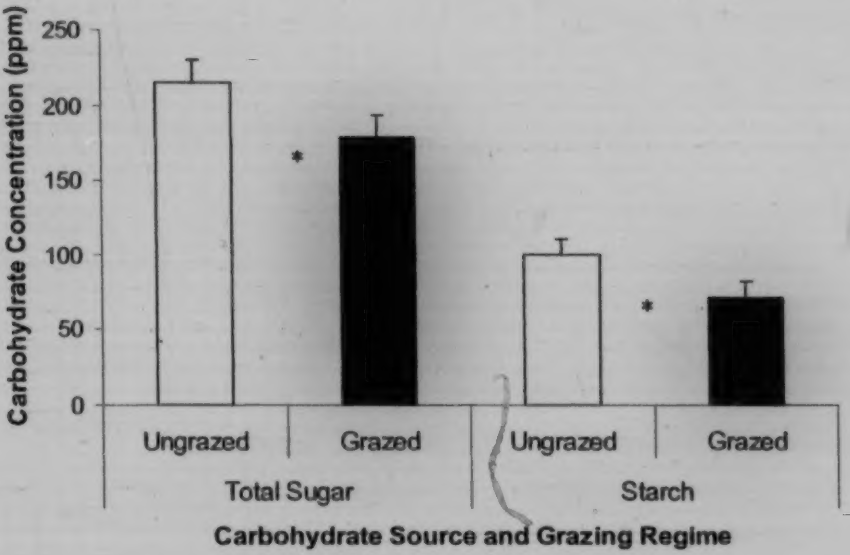

Fig. 4.3: Effects of cattle grazing on mean (± S.E.) *T. latifolia* crown carbohydrate reserves, including total free sugars and starch concentrations in established wetlands at Kitsim. Sampling was conducted in October 2005 after implementing post-treatment reflooding. Within a carbohydrate source, a * indicates grazed and ungrazed treatment means differ ($P < 0.05$).

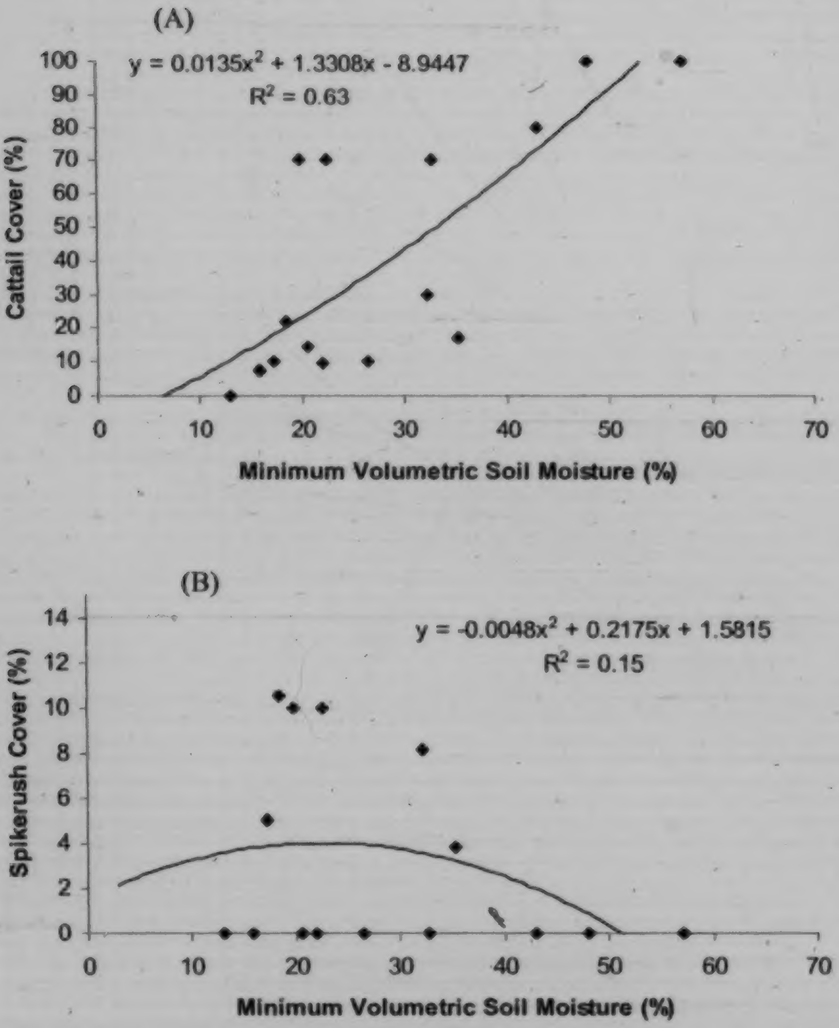

Fig. 4.4: Relationship of the above ground canopy cover of *T. latifolia* (A) and *E. palustris* (B) to volumetric soil moisture at Kitsim during end of flooding treatment sampling in July /August 2004.

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CHAPTER 5

HERBAGE AVAILABILITY AND USE BY CATTLE ALONG HYDROLOGIC GRADIENTS WITHIN CREATED WETLANDS OF THE DRY MIXED GRASS PRAIRIE

5.1. Introduction

Beef production is an important agricultural industry in the grassland regions of Alberta, Canada (Olson 1994, Turnbull et al. 1994). Herbage production and quality are typically variable, both spatially (Willms 1988, Asamoah et al. 2004) and seasonally (Willms and Rode 1998), and these have important implications on cattle foraging behavior across the landscape (Willms 1988, Asamoah et al. 2003). Studies in the Fescue Prairie (Willms 1988), Aspen Parkland (Asamoah et al. 2004) and Boreal (Bork et al. 2001) regions of Alberta indicated that lowland meadows produce greater herbage compared to adjacent uplands, retain greater nutritive quality longer into the summer, and are more frequently used by cattle (Willms 1988, Asamoah et al. 2003).

Although undocumented, these spatial differences are likely to be more pronounced in the Dry Mixed Grass Prairie (DMP) region of southeastern Alberta, Canada, where moisture availability is the primary factor limiting forage production (Willms and Jefferson 1993). Little empirical information currently exists on the spatial patterns of herbage availability and quality, as well as cattle foraging patterns across rangelands in the DMP region, including landscapes containing wetlands created for waterfowl habitat. This information is critical for quantifying the agronomic and economic contribution of these wetlands to cattle production in affected regions.

The DMP is a semi-arid grassland ecosystem with low, erratic precipitation and high summer temperatures (Strong 1992, Adams et al. 2005). The region is characterized by low production with moderate to low forage quality in late summer (Smoliak 1986). Herbage production is seasonally variable, and heavily dependent on the amount of agricultural 'water year' precipitation occurring between the previous fall (September) through to the end of the current growing season (June) (Smoliak 1986).

Ducks Unlimited Canada (DUC), a private non-profit conservation organization, has entered into agreements with irrigation administrations and landowners to create numerous semi-permanent and permanent wetlands intended to enhance waterfowl habitat in the DMP since 1983 (Sankowski et al. 1987). These wetlands have been created and maintained annually by supplemental flooding to augment existing moisture in naturally occurring dry meadows originally dominated by native plant communities such as mesic grasses and forbs (Fig. 5.1). The primary goal of the wetland development project is to arrest the decline of breeding populations of Northern Pintail (*Anas acuta* L.) (Sankowski et al. 1997), which has been associated with intensified agricultural operations and wetland draining in the region (Austin and Miller 1995). Alongside habitat enhancement, an indirect but important benefit of these wetlands has been the development of spikerush (*Eleocharis palustris* L.) communities, which has been noted to be important for cattle foraging (Sankowski et al. 1987).

While the goal of enhancing the availability of waterfowl habitat has been achieved to date using flooding (Sankowski et al. 1987), the continual maintenance of *E. palustris* communities has been challenging (Dave Kay, Ducks Unlimited Canada, *pers. comm.*). Initial wetland development during the first 3 years resulted in more than a 3-fold increase in *E. palustris* production (Sankowski et al. 1987). However, *E. palustris* has since been competitively displaced by *T. latifolia* (*Typha latifolia* L.) in many

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wetlands created over two decades ago. Although a less desirable plant community for wildlife habitat, anecdotal field evidence suggests cattle may voluntarily feed on *T. latifolia* (Appendices XXVI and XXVII). Moreover, the contribution of *T. latifolia* communities to total forage quality on the landscape remains unknown.

Phenologically, *E. palustris* initially responds to annual spring moisture by rapidly initiating growth to form dense stands (Millar 1973). It is however, less tolerant of extreme hydrologic conditions, including prolonged flooding, drought and elevated nutrient levels (Newman et al. 1996, Chapter 3), which may subject the plant to competitive displacement by other, more productive species such as *T. latifolia* (Millar 1973, Sorrell et al. 2002). *T. latifolia* invades fresh water marshes under extended deep flooding and nutrient enrichment, and rapidly increases to form monocultures by displacing existing plant communities (Millar 1973, Grace and Wetzel 1981, Swanson 1987, Swanson 1992, LaBaugh and Swanson 1992, Newman et al. 1996, Chapter 4). While extended flooding enhances *T. latifolia* vegetative and structural growth, the opposite may apply under drought conditions (Millar 1973, Li et al. 2004). Poiani and Johnson (1989) indicated that although vegetation composition and structure in prairie marshes may temporarily change under flooded conditions, these marshes retain viable propagules of native marsh communities for an extended period of time. Following drawdown, these propagules eventually recover and lead to natural marsh restoration (Weinhold and van der Valk 1989).

While plant communities within small riparian meadows and marshes may be uniform (Johnson et al. 1987), larger marshes can be distinctly stratified into communities along hydrologic gradients, including dry marsh, regenerating marsh, degenerating marsh, and lake (van der Valk and Davis 1978). These stratifications may have important implications on spatial herbage growth (Millar 1973) and consequently, cattle foraging opportunities across the landscape. As natural grassland hydrology affects herbage dynamics (Millar 1973, Asamoah et al. 2004) and subsequently, cattle foraging behavior on the landscape (Willms 1988, Asamoah et al 2003), it is important to understand the added impacts of anthropogenic flood augmentation on herbage dynamics, and their contribution to overall cattle foraging potential in the DMP. In newly created wetlands, it is not known how artificial flooding during spring or fall changes patterns of herbage availability, quality and utilization by cattle. Moreover, an important question of interest to land managers is whether anthropogenic induced plant community change from *E. palustris* to *T. latifolia* in established wetlands is reversible with the removal of causal factors (e.g., termination of flooding) (Fig. 4.1) (Boer and Stafford-Smith 2003), which in turn, will change short-term forage availability.

Overall, this study was conducted to determine how wetland moisture regime interacts with cattle grazing to influence spatial and temporal herbage availability, quality and patterns of forage utilization by cattle. Two specific research objectives were addressed. The first involved an assessment of the effects of season and depth of flooding on herbage availability, quality and utilization patterns during early wetland development in the DMP. Second, the effects of changes in anthropogenic flooding frequencies, seasons and water depth on herbage availability, quality and utilization patterns was assessed during hydrologic treatments intended to re-establish *E. palustris* communities from *T. latifolia*-dominated wetlands.

5.2. Materials and Methods

5.2.1. Description of Study Sites

This research was conducted on landscapes associated with newly developed wetlands at the Contra-Costa wetland complex (*aka*. Contra-Costa) and established wetlands at the Kitsim wetland complex (*aka*. Kitsim). Both Contra-Costa and Kitsim are located near the city of Brooks (50° 33' N; 111° 51' W) in the DMP region of southeastern Alberta, Canada. Brooks is an agricultural settlement, relying on irrigation water for crop production. While much of the landscape has been tilled, many native rangelands remain, and are used for cattle grazing, wildlife habitat conservation, recreation, and energy extraction.

Created wetlands in this native landscape are flooded using a gravity-fed irrigation canal system to transport water from reservoirs. Flooding is implemented to develop wetlands using flood control structures, which enables the close regulation of flood regimes, including timing and depth. Flooding at Kitsim has changed considerably since the inception of the project in 1983. Kitsim wetlands were originally flooded three times annually from May to August to maintain permanence. In early 2000, flooding changed to once a year in August / September (i.e., fall) to reduce wetland permanence, with flood depths ranging from 30 to 75 cm (Dave Kay *pers. comm.*). Overall, this change in flood regime resulted in an 11% reduction in the proportion of permanent wetlands, and an increase of 29% in seasonal or temporary wetlands, according to the wetland classification system of Stewart and Kantrud (1971).

In addition to anthropogenic flooding, wetland moisture levels are affected annually by recharge from spring snow melt and growing season rainfall, as well as year-round losses due to evapotranspiration. Annual precipitation at Brooks in 2002 was similar to the long-term annual average of 348 mm. Precipitation in 2003 and 2004 were 23.2% and 14% below the long-term average, respectively, while in 2005, precipitation was 55% above the long-term average. Monthly long-term (30-year) precipitation and temperature, as well as those from 2001 to 2005 are indicated in Appendices I and II, respectively (Environment Canada, Canadian Climate Normals).

5.2.2. Experimental Design and Hydrologic Treatments

A total of 8 and 16 wetlands were selected at Contra-Costa and Kitsim in August 2002, respectively. Wetlands at Contra-Costa were comprised of minimally altered wet or dry meadow communities dominated by *E. palustris*, foxtail barley (*Hordeum jubatum* L.), and western dock (*Rumex occidentalis* S. Wats.), while Kitsim wetlands were heavily dominated by *T. latifolia*.

Different hydrologic treatments (flooding at Contra-Costa, and both flooding and drying at Kitsim) were applied to the selected wetlands from 2002 to 2005, and data collected annually in August. Independent treatment variables manipulated at Contra-Costa included the season of flooding and depth of flooding (topographic position) while at Kitsim, they included flood regime (i.e., season of flooding or duration of drying), the presence of cattle grazing and topographic position.

Under grazing disposition management of the Eastern Irrigation District, both Contra-Costa and Kitsim complexes were annually open to seasonal light to moderate cattle grazing from early summer (June) and mid fall (October).

5.2.2.1. Treatment Implementation at Contra-Costa

New wetland development was assessed at Contra-Costa, where a split-plot design was used to evaluate the effects of annual fall and spring flooding on the spatial and temporal patterns of herbage availability, quality and utilization by cattle. Season of flooding was the main plot, which was stratified into four depths of flooding (topographic position) perpendicular to the landscape profile, with annual herbage sampling in 2002, 2004 and 2005. Herbage utilization was quantified using portable 1.5 x 1.5 m range cages to exclude cattle grazing. Season of flooding had three treatment levels, including artificial fall flooding (FF), artificial spring flooding (SF), and continued natural flooding (NF) from spring snow melt and occasional recharge with heavy growing season rainfall. Of the eight study wetlands at Contra-Costa, four were assigned to FF, two to SF, and two to the NF treatment. Depth of flooding had four levels, including deep flooding (60cm), shallow flooding (30cm), water (i.e., flood) line (0cm), and sub-irrigated upland (-30cm). To assess the impact of various flooding depths on herbage biomass and quality, a 20-m permanently marked transect was established within each of the target flooding depths (n = 32). A Laser Level (Leica Wild LNA 30™) was used to locate each transect. Wetlands receiving the FF and SF treatments were subsequently flooded until target depths were achieved during August /September 2002 or April 2003, respectively, and repeated annually until September 2004 or April 2005 (Appendix III).

5.2.2.2. Treatment Implementation at Kitsim

A split-plot design was used to evaluate the effects of various flooding treatments on the spatial and temporal patterns of herbage availability, quality and utilization at

Kitsim. The main plot was flooding treatment, within which each wetland was divided further into ungrazed and grazed areas. A split occurred within each ungrazed or grazed area into 4 community types, stratified by topographic position across the landscape.

A randomly selected portion of each wetland basin was fenced within 25 x 50 m exclosures to exclude cattle grazing, and enabled comparison of ungrazed and grazed areas. Each of these, in turn, was further stratified into four topographic positions, including sub-irrigated upland, dry meadow, wet meadow and deep marsh zones, as described by Stewart and Kantrud (1971). Permanently marked transects (n = 128) were established to facilitate repeat annual herbage sampling at Kitsim.

The independent variables investigated included flooding (i.e., hydrologic) treatment, cattle grazing and landscape location (i.e., topographic position). Four flooding treatments were examined, including 2-years of no flooding (or flood cessation) with subsequent fall reflooding (2YNF), 1-year of no flooding with subsequent fall reflooding (1YNF), 8-months of initial drying followed by a change to annual spring flooding (SF), and a continuation of the current DUC practice of annual fall flooding (FF). Wetland flood cessation was implemented to increase the likelihood of *T. latifolia* control at Kitsim. Of the 16 study wetlands at Kitsim, four (replicates) were randomly assigned to each flooding treatment implemented from 2002 to 2005 (Appendix IV). All wetlands were set at similar pre-treatment conditions by flooding in either fall 2001 or 2002, depending on the treatment. The 2YNF was achieved by deferring artificial fall flooding in both 2002 and 2003, and subsequently reflooding in the fall of 2004. Similarly, the 1YNF treatment was established by deferring artificial fall flooding in 2003 and then reflooding in the fall of 2004. The SF treatment included deferring fall flooding in 2003 to initiate artificial spring flooding in 2004. The FF treatment continued with annual artificial fall flooding in August/September (i.e., the regular DUC flooding regime). With the exception of the SF treatment, all Kitsim wetlands were reflooded in fall 2004. The SF wetlands were reflooded in spring 2005. The intent of reflooding was to evaluate the impact of all treatments on vegetation through the assessment of post-treatment regrowth.

5.2.3. Herbage Sampling

Four major herbage components, including grasses (graminoids), forbs, *T. latifolia* and *E. palustris*, were sampled along each permanent transect at Contra-Costa and Kitsim. Prior to initial flooding at Contra-Costa, herbage biomass and quality were sampled in August 2002 along all 32 transects. Subsequent herbage sampling was conducted at peak biomass (i.e., July) in 2004 and 2005 during the second and third year of wetland development, respectively. Herbage biomass sampling was conducted by clipping duplicate 0.25 m^2 (0.5 x 0.5 m) quadrats from caged (i.e., livestock removed) and uncaged (i.e., areas exposed to livestock) areas along the permanent transects. Herbage clipping from uncaged locations was ensured to be at least, 5 m from away from the range cage in order to avoid the likelihood of concentrated use around range cages.

At Kitsim, herbage sampling occurred at the end of flooding treatment implementation in 2004, and post-treatment reflooding in 2005, along all 128 permanent transects across grazed and ungrazed areas of the 16 study wetlands. Herbage biomass was sampled with the use of 0.25 m^2 quadrats in both grazed and ungrazed areas. Standing litter was clipped alongside herbage in all 0.25 m^2 sampling quadrats in 2005.

All harvested samples were sorted to grasses (graminoids and grass-likes), forbs, *T. latifolia* and *E. palustris*, and together with litter samples, oven-dried at 35°C for 96 hrs, and weighed to determine dry matter (DM) yield.

Each herbage component was ground to 1 mm through a Wiley Mill™ to facilitate laboratory determination of nitrogen and crude protein (CP) concentration, as well as acid detergent fiber (ADF). Crude protein content of each sample was determined from nitrogen values (%CP = %N x 6.25), with nitrogen derived by the Dumas method using a LECO FP-428 auto-analyzer (Sweeney and Rexroad 1987, Lee et al. 1996). Biomass and CP values were combined to determine the crude protein yield (CPY) associated with each herbage component, with total CPY obtained by summing the CPY of all herbage components within each topographic position (i.e., transect). All CPY measures were determined empirically as the CP fraction of DM yield in g m^{-2} of individual herbage components, using the relationship: (%CP/100)*DM.

The ANKOM™ filter bag technique, as described by Komarek (1993) and Safigueroa et al. (1999), was used to determine the ADF of duplicate forage samples of individual herbage components from each transect.

Biomass assessment at Kitsim represented long-term production under grazed and ungrazed conditions, and therefore, could not be used to assess annual biomass removal through cattle grazing. Consequently, patterns of plant community visitation by cattle were determined following herbage biomass assessments at both Contra-Costa and Kitsim in August 2004. This was done by recording the frequency of plant community (topographic position) visitation by cattle, as of August 14, 2004. Frequency data were determined by counting the number of 0.5 x 0.5 m systematically placed quadrats, out of a total of eight per transect, in which there were visible signs of defoliation presumably caused by cattle or wild herbivores. The use of community visitation to assess utilization patterns became necessary because of the lack of investigator control over cattle grazing (i.e., stocking rates), particularly at Contra-Costa. Notwithstanding this limitation, herbage biomass utilization was quantified at Contra-Costa after cattle grazing ended in October 2005. This assessment was conducted across topographic positions by clipping 0.25 m^2 quadrats both within and outside 1.5 m x 1.5 m range cages, which prevented cattle grazing. Utilization was calculated by subtracting the herbage remaining in grazed areas from that protected from cattle grazing, and expressed in both absolute (g m^{-2}) and relative (%) terms, which are indicative of grazing impacts from the perspective of the grazing animal and plant community, respectively (Bork and Werner 1999).

5.2.4. Statistical Analyses

By virtue of differences in site characteristics, study design and treatment applications, Contra-Costa and Kitsim data were analyzed separately. Pre-flooding (2002) herbage biomass and quality data at Contra-Costa were used as covariates in analyzing the 2004 and 2005 data. Initially, datasets from each location were subjected to normality tests and found to be non-normal ($P > 0.05$). Non-normality was likely due to a smaller sample size (particularly at Contra-Costa) and the presence of many zero biomass values associated with individual herbage components. Thus, to perform statistical data analyses, Contra-Costa biomass and crude protein yield data were log-transformed, while those at Kitsim were square-root transformed (Zar 1999).

Due to the availability of pre-flooding biomass and quality data and the continuity of annual flooding treatment implementation throughout sampling years, Contra-Costa herbage biomass and quality data were analyzed using repeated measures ANCOVA for split-plot designs (Steele et al. 1997, Zar 1999) in Proc Mixed of SAS (SAS Institute Inc. 2003). Thus, Contra-Costa data sets were adjusted for covariate effects based on pre-flooding biomass and quality data. In contrast, no pre-flooding biomass and quality data were available at Kitsim, and sampling occurred at the end of flooding treatment (2004) and post-treatment reflooding (2005) periods. Thus, Kitsim biomass and quality data could not be adjusted for pre-flooding (covariate) effects. Kitsim data were analyzed independently for the 2004 and 2005 sampling years using ANOVA for a split-plot design, as each of the two periods represented end of flooding treatment and post reflooding sampling, respectively. Finally, litter accumulation (Kitsim) and herbage utilization (Contra-Costa) were analyzed using a 2-way ANOVA in Proc Mixed (SAS Institute Inc. 2003).

Unless otherwise specified, treatments were considered significant when the main effects or their interactions had a $P \leq 0.10$. However, multiple LSmean comparisons were made using a more conservative Tukey's test significance value ($P \leq 0.05$) to minimize the risk of type I error.

5.3. Results

5.3.1. Herbage Responses at Contra-Costa

5.3.1.1. Above ground Biomass at Contra-Costa

Above ground grass biomass at Contra-Costa was affected by flooding treatment ($P = 0.009$), topographic position ($P < 0.0001$) and sampling year ($P = 0.0006$), as well as the interaction of flooding treatment × topographic position ($P = 0.11$) and topographic position × sampling year ($P = 0.06$) (Table 5.1).

Overall, naturally flooded (NF) wetlands had the greatest grass biomass compared to artificially flooded (FF and SF) wetlands (Table 5.2). Flooding treatment × topographic position effects indicated that the greatest grass biomass originated from the waterline zones of SF and NF wetlands, as well as upland zones of FF wetlands (Table 5.2). Notably, upland positions of FF wetlands had greater grass biomass than those of SF and NF, and vice versa in the waterline zones (Table 5.2). Also, the shallow flooding zones of NF wetlands had greater grass biomass than those of similar positions under the artificially flooded (FF and SF) condition (Table 5.2). Compared to the NF treatment, the least grass biomass occurred in deep flooding zones of artificially flooded wetlands (Table 5.2).

Between sampling years, grass biomass at Contra-Costa in 2005 was 2.3 times greater than that of 2004 (Table 5.3). Topographic position × sampling year effects indicate that grass biomass was particularly greater in upland, waterline and shallow flooding zones in 2005 compared to the same positions in 2004 (Table 5.3). Grass biomass in the deep flooding zones was similar between the two sampling years. Across topographic positions, grass biomass was greatest in both upland and waterline zones and least in the deep flooding zone (Table 5.4).

Forb biomass was not affected by flooding treatment but varied spatially across topographic positions ($P = 0.009$) (Table 5.1). There were also no interactions among flooding treatment, topographic position and sampling year, on forb biomass ($P > 0.10$) (Table 5.1). Forb growth was limited primarily to upland and waterline zones (Table 5.4) where their average biomass was 17.4 ± 0.8 g m^{-2}.

E. palustris biomass was unaffected by the flooding treatments implemented ($P > 0.10$). Neither did *E. palustris* biomass vary between sampling years ($P > 0.05$). However, there were both position ($P = 0.05$) and flooding × position interaction ($P = 0.10$) effects on *E. palustris* biomass (Table 5.1). Across topographic positions, *E. palustris* biomass generally increased from uplands to the deep flooding zones (Table 5.4). The interaction indicated that the greatest *E. palustris* biomass occurred in the shallow and deep flooding zones of SF wetlands, as well as the waterline and deep flooding zones of FF and NF wetlands, respectively (Table 5.2). Notably, the deep flooding zones of FF wetlands produced less *E. palustris* biomass compared to SF and NF wetlands (Table 5.2).

5.3.1.2. Crude Protein Concentration and Yield at Contra-Costa

At Contra-Costa, flooding treatment affected crude protein (CP) concentrations of grass ($P = 0.10$) but not that of forb or *E. palustris* ($P > 0.10$) (Table 5.1). However, CP concentrations of each of the 3 herbage components did vary across topographic positions ($P < 0.01$) (Table 5.1). Among all vegetation components, only grass varied in CP concentration (P=0.07) between sampling years. There was also a position × year effect on grass CP ($P = 0.01$) (Table 5.1).

The NF treatment resulted in greater grass CP concentration (6.9 ± 1.5 g m^{-2}) compared to both the FF and SF treatments (4.5 ± 0.8 g m^{-2}). Overall CP concentrations of both grass and forb were greatest in the upper topographic positions and progressively declined through lower zones (Table 5.4). In contrast, *E. palustris* CP was greatest in the lower topographic zones and declined with increasing elevation (Table 5.4). Position × year interactions indicate that grass CP within shallow flooding zones during 2005 was more than 5 times greater than the previous year (Table 5.3).

Assessment of crude protein yield (CPY) dynamics at Contra-Costa indicated that grass CPY was affected by flooding treatment ($P = 0.006$), topographic position ($P = 0.0001$), and flooding × position ($P = 0.03$) (Table 5.1). Additionally, grass CPY was affected by sampling years ($P = 0.0004$) (Table 5.1). Trends in grass CPY paralleled that of grass biomass, for example being greatest on NF wetlands (Table 5.2). Across topographic positions, grass CPY was greatest in both upland and waterline zones and least in the deep flooding zone (Table 5.4). Spatial variation in grass CPY also depended on the type of flooding treatment, with the greatest grass CPY in waterline zones of SF and NF wetlands, as well as the shallow flooding zones of NF and upland zones of FF wetlands, respectively (Table 5.2). Compared to the NF treatment, less grass CPY occurred in the deep flooding zones of artificially flooded wetlands (Table 5.2).

Both forb and *E. palustris* CPY at Contra-Costa were unaffected by flooding treatment ($P > 0.10$) but varied spatially across topographic position ($P = 0.11$ and $P = 0.07$, respectively). *E. palustris* CPY was also affected by a flooding × position interaction ($P = 0.09$).

Forb CPY was greatest in the waterline zones (2.1 ± 0.1 g m^{-2}), followed by that of the uplands (1.5 ± 0.1 g m^{-2}), and least in the lower topographic (flooded) zones (Table 5.4). Overall, the greatest *E. palustris* CPY originated from the 2 lower topographic zones with very little from uplands (Table 5.4). Flooding × position effects on *E. palustris* CPY indicated that the greatest *E. palustris* CPY originated from shallow and deep flooding zones of SF wetlands, as well as the waterline and deep flooding zones of FF and NF wetlands, respectively (Table 5.2).

To assess the impact of various flooding regimes on total forage availability (i.e., following plant community changes), individual CPY values from each herbage component were pooled by transect. Total CPY was unaffected by flooding treatment or topographic position ($P > 0.10$). Instead, total CPY varied between the two sampling years ($P = 0.009$), with a topographic position × sampling year interaction ($P = 0.04$). Overall, total CPY in 2005 was greater than in 2004 (Table 5.5). Total CPY generally increased towards the flooded zones in 2004, peaking under deep flooding, while total CPY in 2005 remained similar across the 3 lower topographic positions (Table 5.5).

5.3.1.3. Acid Detergent Fiber (ADF) at Contra-Costa

Grass ADF concentrations at Contra-Costa were affected by flooding treatment ($P = 0.02$), as well as flooding × year ($P = 0.05$) and flooding × position × year ($P = 0.03$) interactions (Table 5.1). Overall, grass ADF levels were greater on FF and NF wetlands than SF wetlands (Table 5.6). Grass ADF levels also changed temporally among flooding treatments, being greatest on FF wetlands in 2004 and NF wetlands in 2005 (Table 5.6). While grass ADF levels on FF wetlands decreased ($P < 0.05$) from 2004 to 2005, primarily due to low ADF levels at the waterline and shallow flooding positions, grass ADF within SF wetlands increased significantly ($P < 0.05$) in 2005 (Table 5.6). ADF levels were most stable in the NF treatment (Table 5.6).

The ADF concentrations of forb and *E. palustris* were unaffected ($P > 0.10$) by flooding treatment, topographic position, sampling year and their various interactions (Table 5.1). Average forb and *E. palustris* ADF were 41.5 ± 0.7% and 43.9 ± 0.7%, respectively.

5.3.2. Herbage and Litter Responses at Kitsim

5.3.2.1. Above ground Biomass Yield at Kitsim

Flooding treatments at Kitsim affected the above ground biomass of grass at each of the 2 sampling periods in 2004 and 2005 ($P \leq 0.10$) (Table 5.7). Grass biomass also varied across topographic positions in both sampling years ($P < 0.0001$), with a flooding treatment × topographic position effect on grass biomass in 2005 ($P = 0.07$) (Table 5.7). Overall, the SF treatment resulted in the greatest grass biomass, both at the end of flooding treatment and during post reflooding (Table 5.8A). Spatially, the greatest grass biomass occurred in upper topographic zones (i.e., uplands and dry meadows) in each of the 2 sampling years (Table 5.8A). The flooding treatment by topographic position interaction in 2005 resulted from high grass biomass in dry and wet meadow zones of SF wetlands, as well as the dry meadow zone of 1YNF wetlands (Table 5.8A). The least grass biomass occurred in the deep marsh zone, particularly of FF, SF and 1YNF wetlands (Table 5.8A).

Similar to grass, forb biomass was affected by flooding treatment in 2004 ($P = 0.004$) and 2005 ($P = 0.06$), as well as topographic position in each of the two sampling periods ($P < 0.0001$) (Table 5.7). Forb biomass also had a flooding × topographic position effect in both years ($P < 0.1$) (Table 5.7). Overall, the 2YNF treatment resulted in the greatest forb biomass, both at the end of flooding treatment and post reflooding (Table 5.8B). Spatially, the greatest forb biomass occurred in wet meadow zones during each year, although dry meadows were similarly high in 2005. Forb biomass on uplands was very low (Table 5.8B). Flooding treatment × topographic position interactions indicated that the release of forb biomass in 2YNF wetlands, and to a lesser extent 1YNF wetlands, during 2004 originated from the wet meadow and deep marsh zones. This increase persisted into 2005, but only in the 2YNF wetlands. While forb biomass was consistently low in dry meadows and uplands, FF treatments tended to have more forbs at this position relative to the other flooding treatments in both years. Following post reflooding, the greatest forb biomass was evident in wet meadow zones of 2YNF wetlands with the least in deep marsh zones of FF, SF and 1YNF wetlands (Table 5.8B).

Flooding treatments affected *E. palustris* biomass in both 2004 ($P = 0.05$) and 2005 ($P = 0.11$) (Table 5.7), as did topographic position in both sampling years ($P < 0.05$) (Table 5.7). In both years, the greatest *E. palustris* biomass was evident within 1YNF wetlands and the least in FF and 2YNF wetlands (Table 5.8C). Across the landscape, *E. palustris* biomass was concentrated in deep marsh zones during 2004, mostly in the SF and 1YNF treatment. In 2005 following reflooding, *E. palustris* biomass extended into wet meadow zones, specifically SF and 1YNF wetlands (Table 5.8C).

The biomass of *T. latifolia* demonstrated flooding ($P < 0.05$), topographic position ($P < 0.0001$) and flooding x position ($P < 0.01$) effects in both years of sampling at Kitsim (Table 5.7). As expected, *T. latifolia* biomass was greatest in deep marsh zones, with intermediate amounts in wet meadows (Table 5.8D).

Among flooding treatments, FF wetlands had the greatest *T. latifolia* biomass in 2004, followed by SF wetlands, and then those areas receiving drying for 1 or 2 years (Table 5.8D). In the latter 2 treatments, *T. latifolia* was nearly eliminated within the wet meadow position. In 2005, while 1YNF and 2YNF wetlands remained low in *T. latifolia*, the greatest biomass of this species occurred on SF wetlands (Table 5.8D). In both sampling years, the least *T. latifolia* occurred on 2YNF wetlands, which included a 95.7 % reduction in *T. latifolia* biomass in 2004 compared to that of the FF treatment. Although *T. latifolia* exhibited some recovery with reflooding, as indicated by the near 3 fold increase in biomass in 2005, *T. latifolia* biomass remained lower ($P < 0.05$) than all other treatments in that year (Table 5.8D). Recovery of *T. latifolia* was particularly poor in the deep marsh zone of 2YNF wetlands. Finally, a marked increase in *T. latifolia* was evident in 2005 within SF wetlands at the deep marsh position.

5.3.2.2. Grazing Effects on Above ground Biomass at Kitsim

Grass biomass was affected by grazing treatments in each of the 2 sampling years ($P < 0.0001$ for 2004, and $P = 0.01$ for 2005, respectively), as well as by the grazing x flooding interaction in 2005 ($P = 0.07$) (Table 5.7). In 2004 average grass biomass in ungrazed areas was more than twice that of grazed locations (Table 5.9). However, in 2005 following reflooding, this pattern reversed, with ungrazed areas lower in grass biomass. Reductions in grass biomass in the absence of grazing were particularly evident in the FF and 1YNF treatments.

Forb biomass was also affected by grazing in both 2004 ($P < 0.0001$) and 2005 ($P < 0.10$), as well as by the interaction of grazing × topographic position in 2004 (Table

5.7). Similar to grasses, ungrazed sites had greater forb biomass in 2004, with the reverse occurring in 2005 (Table 5.10). Decreases in forb biomass in 2004 with grazing were confined to the dry meadow and wet meadow zones. This further reinforces that in 2004, production was water limited, but not in 2005.

E. palustris biomass had a grazing × flooding effect ($P = 0.002$) in 2004 and a lone grazing effect ($P = 0.05$) in 2005 (Table 5.7). In 2004, *E. palustris* biomass was greater with grazing in the SF treatment, but lower with grazing in 1YNF wetlands. Notably, *E. palustris* was absent in both ungrazed and grazed sites of 2YNF wetlands in 2004 (Table 5.11). In 2005 ungrazed sites had less *E. palustris* compared to grazed sites, parallel that of other herbage (Table 5.11).

T. latifolia biomass was unaffected by grazing ($P > 0.10$) (Table 5.7). However, grazing interacted with topographic position to affect *T. latifolia* biomass in both 2004 ($P = 0.11$) and 2005 ($P = 0.10$) (Table 5.7). Grazing led to decreased *T. latifolia* in 2004, but only in deep marsh zones, with a reversal in 2005 when reflooded wet meadows and deep marsh zones had more *T. latifolia* in grazed locations (Table 5.12).

5.3.2.3. Crude Protein (CP) Concentration at Kitsim

Grass CP concentration was unaffected by flooding treatment and topographic position in 2004 ($P > 0.10$) (Table 5.7), averaging 8.2 ± 0.3%. Following post reflooding in 2005, grass CP varied spatially across topographic positions ($P = 0.0003$) (Table 5.7), ranging from a high of 9.3 ± 0.3% on uplands to an average of 7.5 ± 0.4% in the lowest topographic position. Grass CP at Kitsim also varied due to grazing within topographic positions ($P = 0.06$), being greater in grazed locations on uplands (9.9 ± 0.4%) compared to ungrazed uplands (8.7 ± 0.4%), but similar between ungrazed and grazed locations in the dry meadows (7.2 ± 0.2%), as well as the wet meadow (8.0 ± 0.01%). Overall, there was no difference ($P > 0.10$) in grass CP between ungrazed and grazed locations at Kitsim following reflooding in 2005, averaging 8.2 ± 0.1%.

Forb CP was affected by flooding at the end of treatment implementation in 2004 ($P = 0.01$) (Table 5.7). Forb CP also varied across topographic positions in both 2004 ($P = 0.03$) and after reflooding in 2005 ($P = 0.02$) (Table 5.7). In 2004, the 1YNF treatment resulted in the greatest forb CP, while the least was associated with the 2YNF (Table 5.13). Spatially, forb CP peaked in the deep marsh and remained similar across the 3 upper topographic positions (Table 5.13). In 2005, spatial patterns of forb CP changed markedly, with the deep marsh accounting for the least forb CP concentration and uplands the most (Table 5.13). Grazing also influenced the forb CP at Kitsim in 2005 ($P = 0.05$), with ungrazed areas greater in CP concentration (10.0 ± 0.4%) than grazed areas (9.0 ± 0.4%).

E. palustris and *T. latifolia* were only found within the wet and dry meadow zones at Kitsim. *E. palustris* CP concentration was unaffected by flooding treatment and topographic position in 2004 and 2005 ($P > 0.10$) (Table 5.7), averaging 11.9 ± 0.6% and 11.6 ± 0.5% for each sampling period, respectively. *T. latifolia* CP was affected only by flooding treatment in 2004 ($P = 0.07$) (Table 5.7). *T. latifolia* CP in 2004 was greater ($P < 0.05$) on 1YNF wetlands (12.7 ± 1.1%) than all other wetlands (combined average of 7.7 ± 1.1%). Following reflooding in 2005, *T. latifolia* CP averaged 9.1 ± 0.6% across all flooding treatments and topographic positions.

5.3.2.3. Crude Protein Yield (CPY) at Kitsim

Grass CPY was affected by flooding ($P = 0.02$), topographic position ($P = 0.10$) and a flooding × position interaction ($P = 0.03$), but only in 2005 (Table 5.7). Average grass CPY in 2004 was 17.6 ± 0.9 g m^{-2}. Overall, grass CPY in 2005 was lower within 2YNF wetlands compared to most other flooding treatments (Table 5.14A). Grass CPY was similar among flooding treatments at the upland position, but generally greater in meadows of the SF treatment. In contrast, grass CPY was lower in deep marsh zones where these data were available for only 2 flooding treatments (Table 5.14A). Grass CPY in 2005 was also affected by grazing ($P = 0.04$) and the interaction of grazing x flooding ($P = 0.04$) (Table 5.7). Grazed areas were greater in grass CPY, although this effect was limited to the 1YNF wetlands only.

Forb CPY varied spatially across topographic positions in both 2004 ($P = 0.02$) and 2005 ($P = 0.11$) (Table 5.9). In both years forb CPY was lowest within uplands and increased towards lower topographic positions (Table 5.18).

In 2004, *E. palustris* CPY at Kitsim was affected only by topographic position ($P = 0.009$) (Table 5.7). On average, *E. palustris* CPY in the deep marsh (19.8 ± 1.2 g m^{-2}) was greater ($P < 0.05$) than that in the wet meadow zone (15.5 ± 4.0 g m^{-2}), with *E. palustris* absent at the 2 remaining positions. In 2005 both flooding treatment ($P = 0.03$) and topographic position ($P = 0.004$) affected *E. palustris* CPY (Table 5.7). The 1YNF treatment had greater ($P < 0.05$) *E. palustris* CPY (47.1 ± 6.2 g m^{-2}) compared to the SF (28.2 ± 7.4 g m^{-2}) and 2YNF (28.2 ± 4.2 g m^{-2}) treatments, which in turn, were greater ($P < 0.05$) than the FF treatment (12.7 ± 1.5 g m^{-2}). Spatially, average *E. palustris* CPY in the deep marsh zones (41.5 ± 6.3 g m^{-2}) was greater ($P < 0.05$) than that of both dry meadow (28.1 ± 12.8 g m^{-2}) and wet meadow (28.6 ± 6.6 g m^{-2}) zones, with no *E. palustris* on uplands.

T. latifolia CPY at Kitsim was only affected by the flooding treatments (P = 0.004) in 2005 (Table 5.7). The FF and SF treatments resulted in similar *T. latifolia* CPY of 46.1 ± 4.6 and 52.1 ± 7.5 g m^{-2}, respectively, both of which were greater ($P < 0.05$) than the 1YNF treatment (26.1 ± 3.5 g m^{-2}). *T. latifolia* CPY was lowest ($P < 0.05$) in the 2YNF wetlands (13.7 ± 3.4 g m^{-2}).

At the end of flooding treatment implementation in 2004, total herbage CPY at Kitsim was unaffected by flooding treatment ($P > 0.10$) but varied spatially across topographic positions ($P = 0.001$). Total CPY was greater ($P < 0.05$) in the deep marsh (48.1 ± 7.7 g m^{-2}) and wet meadow zone (59.7 ± 7.7 g m^{-2}) than elsewhere in the landscape. Additionally, dry meadows (29.4 ± 7.7 g m^{-2}) had greater total CPY than uplands (15.1 ± 7.7 g m^{-2}). In 2005, total CPY was affected by flooding treatment (P = 0.001), topographic position ($P < 0.0001$), and a flooding × position interaction (P = 0.02). Overall, the 2YNF wetlands had lower total CPY than the other treatments (Table 5.16). Spatially, the greatest total CPY originated from wet meadows and the least from uplands and dry meadows (Table 5.16). Flooding × position effects indicated total CPY to be high in wet meadows of SF wetlands, and low in dry meadows of SF wetlands (Table 5.16). Uplands were more consistent in total CPY across flooding treatments.

5.3.2.4. Acid Detergent Fiber (ADF) at Kitsim

Average grass ADF concentration in 2004 was 45.4 ± 0.2%. Grass ADF was only affected by flooding treatment ($P = 0.008$) and topographic position ($P = 0.05$) in 2005

(Table 5.7). Grass ADF in the latter year was lower on FF wetlands compared to all others (Table 5.17A). Grass ADF was also lowest on uplands and increased towards low-lying topographic positions (Table 5.17A).

Forb ADF levels varied spatially across topographic positions in 2004 ($P = 0.006$) and 2005 ($P < 0.0001$) (Table 5.7). Forb ADF was also affected by flooding treatment in 2005 ($P = 0.09$). In 2004, greater ($P < 0.05$) forb ADF was found in the deep marsh zones (48.3 ± 2.3%) compared to more elevated positions ($x = 41.0 \pm 0.7\%$). A similar trend was evident in 2005, with more separation among landscape positions (Table 5.17B). Forb ADF was also greater on FF and 1YNF wetlands in 2005 compared to the SF and 2YNF treatments (Table 5.17B).

E. palustris ADF was unaffected by flooding treatment and topographic position in each of the sampling years ($P > 0.10$) (Table 5.7), averaging 43.5 ± 0.7% in 2004 and 42.3 ± 0.9% in 2005. However, *E. palustris* ADF varied in response to grazing x position ($P = 0.10$), with *E. palustris* having greater ($P < 0.05$) ADF in ungrazed locations at the wet meadow zone (44.3 ± 0.7%) than grazed locations (42.8 ± 0.7%), while the reverse occurred in deep marsh zones (38.4 ± 0.7% for ungrazed vs. 39.9 ± 0.7% for grazed).

T. latifolia ADF was affected only in 2005 by flooding treatment ($P = 0.05$) and topographic position ($P = 0.11$) (Table 5.7). Average *T. latifolia* ADF in 2004 was 46.5 ± 1.3%. One year later, *T. latifolia* ADF was least on 2YNF wetlands with the other 3 flooding treatments resulting in similar ADF levels (Table 5.17C). *T. latifolia* ADF in the deep marsh zones was also greater than those in wet meadows (Table 5.17C).

5.3.2.5. Litter Accumulation at Kitsim

The amount of litter mass present across wetlands at Kitsim was not affected by the flooding treatments implemented ($P > 0.05$). However, litter mass did vary across topographic positions ($P < 0.0001$), with the greatest accumulation in dry and wet meadow zones (Fig. 5.2). Upland and deep marsh zones retained the least litter.

5.3.3. Livestock Use

5.3.3.1. Absolute and Relative Herbage Utilization at Contra-Costa

Flooding treatment affected absolute ($P = 0.03$) and relative ($P = 0.02$) herbage utilization at Contra-Costa. In addition, variation in absolute ($P = 0.01$) and relative ($P = 0.02$) utilization occurred across topographic positions. However, there was no flooding treatment × topographic position interaction on measures of either absolute or relative utilization ($P > 0.05$). Absolute and relative utilization patterns among treatments were similar, being greater on both fall and spring wetlands compared to natural wetlands (Tables 5.18A and 5.18B, respectively). Spatially, the greatest herbage utilization (absolute and relative) occurred within shallow flooding zones (Tables 5.18A and 5.18B).

5.3.3.2. Plant Community Visitation Under Grazing

Frequency counts of cattle visitation to plant communities across the landscape indicated that cattle uniformly visited all plant communities at both Contra-Costa ($P = 0.44$) (Fig. 5.3A) and Kitsim ($P = 0.58$) (Fig. 5.3B). Overall, frequencies of community visitation were 29.1 ± 3.9% at Contra-Costa and 45.3 ± 3.9% at Kitsim, respectively.

5.4. Discussion

Rangeland cattle production is heavily dependent on the availability of abundant and palatable high quality forage, and studies on cattle foraging behavior have indicated that cattle will maximize intake of readily available and palatable high quality forage in lower topographic zones, prior to utilizing those on uplands (Mueggler 1983, Willms 1988, Asamoah et al 2003). Results of this study indicate that anthropogenic flooding is an important factor causing changes in herbage type, availability and quality, as well as livestock foraging patterns on landscapes associated with created wetlands in the Dry Mixed Grass Prairie. In particular, there were strong spatial differences in herbage type, biomass and crude protein yield across the study landscapes at both Contra-Costa and Kitsim study sites. Similarly, spatial differences in herbage biomass have been documented under natural landscape conditions in the Fescue Prairie (Willms 1988), Aspen Parkland (Asamoah et al. 2004) and Boreal grasslands (Bork et al. 2001) of Alberta, where moisture gradients cause uplands to be less productive compared to lowland meadows. Herbage type, biomass and crude protein yield results in the present study highlight these spatial dynamics and indicate the economic importance of ceated wetlands, which represent 15% of the regional landscape, to livestock foraging.

5.4.1. Herbage Responses and Utilization at Contra-Costa

Moisture availability resulting from the various flooding treatments affected the dynamics of grass (graminoids), forb and *E. palustris* production across topographic zones of newly created wetlands at Contra-Costa. However, forb biomass was very minimal and represented only 3% of total herbage production on the study landscapes.

Fall flooding favored grass production on sub-irrigated uplands, while spring and natural flooding were favorable for grass production in the waterline zones. This pattern suggests that moisture retention in wetlands flooded the previous fall may have removed many grass species in the intervening winter, presumably by creating anaerobic conditions detrimental to most grass species found in waterline zones or lower in the landscape (Mitsch and Gosselink 2000, Chapter 4). Overall, grass biomass represented 49% of total herbage on the study landscapes at Contra-Costa. In particular, there was greater grass production on sub-irrigated uplands of fall flooded wetlands. Typical grass species found on sub-irrigated uplands were xeric species such as *Stipa comata* and *Poa pratensis* (Chapter 4), and according to Coupland and Johnson (1965), xeric upland grasses in the region have deep rooting systems and are capable of accessing water from phreatic depths. The present results suggest that previous fall flooding caused water tables to be elevated such that these normally xeric upland species had ready access to moisture the following spring to facilitate rapid growth and increased biomass production, confirming the results of Smoliak (1986) who indicated that moisture additions from September (previous fall) provides the effective moisture critical for the current year's production in the Dry Mixed Grass Prairie.

Increased grass production in the shallow flooding and waterline zones of spring and natural wetlands is an important observation of the present study. Grasses in the waterline zone consisted mainly of hydric species such as *Agrostis scabra, Hordeum jubatum, Poa palustris,* and *Puccinellia nuttaliana*, all of which increased in relative abundance (Chapter 4), and consequently, led to greater biomass production in response to spring moisture. There was also greater grass production in the shallow flooding and waterline zones of natural wetlands compared to the same positions on spring wetlands. This suggests that although additional spring moisture may facilitate grass production in lower topographic zones, more modest moisture additions from natural flooding in spring appeared optimal for increasing grass production in the shallow flooding and waterline zones. This is not surprising, given that these communities have developed under the natural flood regime of the region, and suggests the artificial flooding regimes tested here may generally have been too high to optimize grass yields.

Overall, marked reductions in grass biomass occurred in shallow and deep flooding zones of newly created wetlands receiving anthropogenic flooding treatments, being replaced with a rapid increase in biomass of *E. palustris*. *E. palustris* has been observed to rapidly increase in cover (Chapter 4) and biomass with initial flood augmentation during wetland development in the DMP region (Sankowski et al. 1987). Overall, *E. palustris* biomass represented 48% of total herbage on the study landscapes at Contra-Costa. The enhancement of *E. palustris* production, particularly in lower topographic zones suggests this plant requires greater moisture for initial establishment (Millar 1973, Sorrell et al. 2002, Chapter 3). Sankowski et al. (1987) reported a 3-fold increase in *E. palustris* within three years of initial shallow flooding in the DMP region. Notably, the greater *E. palustris* production in the present study may be due to the fact that flooding depths were shallower (60 cm maximum) as deep flooding has been noted to be detrimental to a related species - *E. sphacelata* (Sorrell et al. 2002). In addition, the present study was limited to only three years in duration, and plant community succession had not progressed to the point where *E. palustris* was susceptible to competitive displacement by *T. latifolia* (Chapter 4).

Herbage quality results provided valuable insight into the economic benefits of anthropogenic flooding for cattle production in the region. The dynamics of crude protein (CP) concentration, crude protein yield (CPY) and acid detergent fiber (ADF) of the herbage types assessed at Contra-Costa provided insight into their relative contributions to overall forage quality, as well as the potential role of various topographic positions in affecting cattle foraging behavior. A high CP level is indicative of high quality forage (Goering and Van Soest 1970), with CPY quantifying the relative abundance of CP in the herbage types assessed. On the other hand, a high ADF is indicative of high lignin content and low digestibility (Goering and Van Soest 1970), and is thus indicative of low quality forage. The levels of CP and ADF are important measures of forage quality and the average requirements for lactating beef cow are 12 and 38%, respectively (NRC 1996). Results of the study indicated that CP levels of all herbage types, irrespective of the flooding treatment or topographic position, were lower than the average minimum requirement for lactating cows, although spatial increases occurred toward lower topographic zones. ADF levels obtained in the study were also higher than the minimum requirement for lactating cow. Overall, these results indicate that herbage quality was generally poor. Asamoah et al. (2004) noted season-long declines in CP levels in all topographic zones in the Aspen Parkland by nearly 50% from May to July. Although season-long changes in CP were not assessed in the present study, it can be argued that temporal declines in herbage CP occurred in all topographic positions, which probably accounted for the low quality of herbage sampled annually in July of the study years. However, the greater spatial variability of biomass among herbage components led to differential patterns of herbage CPY on the landscape.

Notably, CPY dynamics of all herbage components among flooding treatments paralleled those of herbage biomass, and was further influenced by flooding treatment and topographic position. In particular, natural flooding resulted in the greatest level of grass CPY in upper topographic zones, while *E. palustris* CPY was greatest in the lower topographic zones, especially under spring flooding. Greater grass biomass on upper topographic zones at Contra-Costa, and in particular, the abundant *E. palustris* biomass in lower topographic zones, led to high levels of total CPY, concentrated largely in the lower three topographic positions, peaking in the waterline zone.

The dynamics of herbage biomass, CP and CPY have important implications on cattle foraging behavior on the landscape. Studies in the Fescue Prairie (Willms 1988) and Aspen Parkland (Asamoah et al. 2003) have indicated that cattle may preferentially forage in the lower topographic zones prior to utilizing uplands as a result of higher forage availability, CP and consequently, CPY in the lower topographic zones (Asamoah et al 2004). Results of the present study indicated that flooded wetlands (both spring and fall) at Contra-Costa received greater absolute and relative cattle utilization, especially within the shallow flooding zones, which has greater herbage biomass and CPY levels. Thus, anthropogenic flooding has the benefit of enhancing cattle foraging opportunities through provision of abundant high quality forage, especially in lower topographic zones of newly developed wetlands. The uplands and shallow flooding zones received light and moderate levels of use, respectively. However, cattle ultimately visited all communities across the landscape associated with the study wetlands at Contra-Costa to utilize the available forage. Studies in the Aspen Parkland found that cattle frequently utilized lower topographic zones because of the greater forage availability and quality (Asamoah et al. 2004). Results of the present study on created wetlands in the DMP support this finding and indicated that cattle utilized herbage in lower topographic zones at Contra-Costa in greater abundance than the uplands, likely because of the greater abundance and high quality of *E. palustris*. However, cattle also foraged in all other topographic zones to utilize the available forage. Overall, cattle utilized fall and spring flooded wetlands (moderate use) to a greater extent than natural wetlands (light use), suggesting that flooding at Contra-Costa attracted cattle into those areas, presumably due to enhanced cattle foraging opportunities.

5.4.2. Herbage Responses and Utilization at Kitsim

At Kitsim, season of anthropogenic flooding and length of flood cessation had important impacts on the availability and quality of herbage types found across topographic positions. Not surprising for this environment where water availability limits plant growth (Willms and Jefferson 1993), grass constituted 38% of total herbage production at the end of treatment implementation in 2004, and its biomass was greater on wetlands with continuous flooding than those of flood cessation. In particular, grass production was greatest in the upper topographic zones, especially on SF wetlands, and least in the deep marsh zones of all study wetlands. Similar to the results on fall and spring flooded wetlands at Contra-Costa, moisture availability on FF and SF wetlands at Kitsim enhanced grass production in upper topographic zones likely via sub-surface moisture increases. On the other hand, reduced moisture on 1YNF and 2YNF wetlands may account for the 40% decline in grass production with flood cessation. Following reflooding in 2005, grass production doubled in the upper three topographic zones, affirming the important effect of moisture availability for this herbage component in the Dry Mixed Grass Prairie. Between FF and SF wetlands, there was greater grass production in the wet meadow zones of SF wetlands in both 2004 and 2005 (Table 5.8A), parallel to observations made on fall and spring wetlands at Contra-Costa. As previously indicated, this may be due to the timing of the two flooding treatments and the differential response of hydric grass species in wet meadow zones to high moisture availability in winter and spring.

Although forb production was low compared to grass, its biomass constituted 23% of total herbage at the end of flooding treatment. There was a greater presence of forbs in the lower three topographic zones, especially on 2YNF wetlands in each of 2004 and 2005. Notably, the various species of forbs on the regional landscape have a wide range of rooting characteristics ranging from extensive lateral root system with wide surface area coverage to deep tap root system with access to moisture from phreatic depths (Coupland and Johnson 1965). Thus, the readily available moisture within soils of non-flooded topographic zones appeared to favor forb growth. Non-flooded topographic zones had soil moisture levels, aerobic conditions and insolation levels that favored forb growth from the soil seed bank (van der Valk and Davis 1978). However, excessive soil moisture associated with flooded topographic zones may result in anaerobic conditions detrimental to most forb species (van der Valk and Davis 1978, Mitsh and Gosselink 2000).

Assessment of *E. palustris* production indicated the biomass of this species to be low compared to that of grass and constituted only 3% of total herbage biomass on the study landscapes at Kitsim. Notwithstanding, the greatest *E. palustris* biomass occurred on 1YNF wetlands, followed by SF wetlands at the end of flooding treatment in 2004 and again during reflooding in 2005. The presence of *E. palustris* on 1YNF and SF wetlands illustrates the importance of short-term flood cessation on *E. palustris* recovery (Table 5.8C). While flood cessation was implemented on the 1YNF wetlands for a complete year, it was also implemented on SF wetlands for 8 months prior to switching to spring flooding (Appendix IV). Thus, the short-term flood cessation on both 1YNF and SF wetlands may have equally benefited *E. palustris*. It is important to note that excessive flooding over a long period of time may eventually results in reduced *E. palustris* productivity through competitive displacement by more aggressive species such as *T. latifolia* (Millar 1973, Sorrell et al. 2002), as affected by changes in soil nutrient dynamics (Chapter 4).

Production of *E. palustris* was also concentrated in the wet meadow and deep marsh zones of 1YNF wetlands in each of the two sampling periods. With respect of SF wetlands, while greater *E. palustris* production occurred in the deep marsh zones in 2004, a switch occurred in 2005 with greater *E. palustris* found in the wet meadow zones. The greater *E. palustris* biomass in the deep marsh zones of SF wetlands in 2004 is likely due to the immediate response to moisture availability following the short-term (8-month) flood cessation prior to the implementation of the SF treatment. However, continued implementation of the SF treatment in 2005 likely resulted in excessive moisture in the deep marsh zones, which enhanced *T. latifolia* production at the expense of *E. palustris*, and shifted the distribution of *E. palustris* higher up into the wet meadow zone. This rapid change in *E. palustris* in the landscape also highlights the transitory nature of this species within wetland communities, and it is indicative of the interplaying effects of soil moisture and nutrient dynamics (Chapter 4). The propagules for transition to the new communities may have originated from the soil seed bank (van der Valk and Davis 1978) and other sources such as animal movement and flood waters.

Notably, the 2YNF wetlands consistently had the least *E. palustris* biomass, both in 2004 and 2005, suggesting that two or more years of flood cessation on wetlands heavily dominated by *T. latifolia* may have resulted in too much soil drying for this species, otherwise known to be drought intolerant (Chapter 3). Moreover, this reduction was not offset by subsequent reflooding, with minimal recovery in the wet meadow zones of 2YNF wetlands in 2005 (Table 5.8C).

Overall, *T. latifolia* biomass was greatest on continuously flooded wetlands (FF and SF treatments) and least on flood cessation wetlands, particularly the 2YNF in 2004. Excessive moisture in created wetlands of the Dry Mixed Grass Prairie may provide the optimum conditions for increased *T. latifolia* production (Chapter 3). However, *T. latifolia* demonstrated the most sustained increase in wetlands receiving the SF treatment. These results suggest that *T. latifolia* production is strongly dependent on not only moisture availability (Millar 1993), but also the seasonality of moisture supply as spring flooding led to greater *T. latifolia* production compared to fall flooding. The reason for this disparity is unclear, as flooded environmental conditions and soil nutrient, especially phosphorus levels remained similar under the two flooding treatments (Chapter 4). It may be speculated that the short term flood cessation prior to the implementation of the SF treatment (Appendix IV) may have caused short-term soil aeration beneficial for root respiration in many plant species. Notwithstanding, *T. latifolia* has a unique capacity of maintaining oxidized rhizosphere around its root system under anaerobic conditions by transporting oxygen from the leaves and stems to the roots (Chabbi et al. 2000).

The present results indicated that cessation of flooding for at least two years heavily reduced *T. latifolia* biomass by up to 95.5% compared to that of flooded wetlands. Some authors have indicated the possibility of using drawdown to manage wetland vegetation (Millar 1973, Grace and Wetzel 1981, Weinhold and van der Valk 1989, Li et al. 2004). This observation was affirmed for *T. latifolia* with at least two years of flood cessation. However, minimal increases in *T. latifolia* biomass occurred within 2YNF wetlands following reflooding during 2005. This suggests that while two years of flood cessation was capable of causing significant declines in *T. latifolia* production, the plant has the potential to recover when flooding resumes, as was previously found (Chapter 3, Chapter 4).

Results of the study indicated that areas exposed to cattle grazing had reduced biomass production of all herbage components under study in 2004, including grass (55%), forb (72%), *E. palustris* (60%) and *T. latifolia* (37%). These suggest that each of the four herbage types assessed contributed to cattle foraging at Kitsim, with forb receiving the greatest level of utilization. Notably, the greatest level of forb utilization over the period occurred in the wet meadow zones where it occurred in greatest abundance. Although, *E. palustris* received the next greatest level of utilization after forb, its minimal contribution to total herbage biomass made it less economically important for cattle foraging at Kitsim, compared to grass and forb. It is important to note that, although *T. latifolia* is not a typical forage species for cattle, areas exposed to long-term cattle grazing had reduced *T. latifolia* biomass by more than a third at Kitsim

(Appendices XXVI and XXVII). However, with subsequent reflooding, grazed areas at promptly recovered and produced greater biomass of all herbage components than areas excluded from grazing. Donkor et al. (2002) found in a laboratory study that, defoliated *Bromus-Poa* grass mix increased in biomass under increased soil moisture. Results of the present study may confirm this observation, and suggest that herbage removal by cattle helped reduce litter and stimulated plant regrowth with subsequent reflooding.

The dynamics of grass CPY at Kitsim did not indicate significant treatment effects except after reflooding in 2005 when the 2YNF wetlands had the least CPY levels. Lower grass CPY levels on 2YNF wetlands were likely caused by the low overall grass biomass associated with 2YNF wetlands. Spatially, the least grass CPY originated from deep marsh zones, likely because of a lack of grass species in this topographic position. Notably, grazed areas had greater grass CPY than areas excluded from grazing. This probably occurred because of greater grass biomass in grazed areas, especially following reflooding in 2005.

Similar to Contra-Costa, the CP and ADF levels of the four herbage types assessed at Kitsim did not meet the minimum nutritional requirements of lactating beef cattle, likely because sampling occurred in July when significant reductions in forage quality had occurred (Asamoah et al. 2004). Although *T. latifolia* had a lower CP concentration compared to the other herbage types, this plant maintained greater CPY in the wet meadow and deep marsh zones, especially on fall and spring flooded wetlands, leading to very high total herbage CPY at Kitsim. *T. latifolia* dominated wetlands appeared to have very high CPY levels, with the present results together with that of Chapter 4 indicating that cattle utilized *T. latifolia* to some extent. These results suggest that, while *T. latifolia* may be less preferred as forage, cattle may utilize the species likely because of the abundant source of CPY. However, wetlands heavily infested *T. latifolia* may not be economically useful for cattle production because of minimal long-term utilization levels found in the present study.

5.5. Conclusions and Management Implications

Although herbage production in xeric to mesic upland and meadow sites were enhanced with artificial flooding in the Dry Mixed Grass Prairie, herbage biomass and quality were spatially variable depending on the amount (depth) of flooding. Spring and natural flooding on newly developed wetlands at Contra-Costa resulted in greater biomass of hydric grasses in the shallow flooding and waterline zones, compared to fall flooding. Initial flooding resulted in abundant high quality *E. palustris* production in the lower topographic zones. A spatial tradeoff occurred between grass and *E. palustris* biomass from uplands to the deep flooding zones, with marked reductions in grass biomass in shallow and deep flooding zones, and being replaced with a rapid increase in biomass of *E. palustris*. Although herbage quality fell short of the minimum requirement for lactating cows, crude protein yields were spatially oriented and increased towards lower topographic zones. Cattle appeared to utilize the lower topographic zones to the largest extent, although the entire landscape was also utilized.

The biomass and quality of herbage components in existing *T. latifolia* dominated wetlands were spatially and temporally variable depending on how long flooding was withheld. Flood cessation or drawdown was found to be effective in limiting *T. latifolia* production on affected wetlands. However, under the conditions of this short-term study, there was no guarantee that flood cessation used to control *T. latifolia* could help facilitate complete recovery of *E. palustris*. Instead, *T. latifolia* has a greater chance of recovery when the affected wetlands were reflooded after two years of flood cessation. *E. palustris* occurred in the least abundance among the four herbage types assessed.

Utilization assessment indicated that all four herbage components were utilized by cattle, though in varying proportions. Moreover, *T. latifolia* may not substitute the originally displaced *E. palustris* in providing palatable forage for cattle, though it appears to have very high crude protein yield level.

To promote sustainable wetland development and livestock production on artificially flooded wetlands in the Dry Mixed Grass Prairie, there is the need for careful flood water management during initial wetland development as suggested in Chapter 4. This will help establish and maintain *E. palustris* production for use as forage and cover for both livestock and wildlife in the region.

Table 5.1: Summary of statistical tests indicating *P*-values on the effects of flooding treatment and depth (topographic position) on above ground biomass, crude protein, crude protein yield and acid detergent fiber (ADF) of grass, forb and *E. palustris* sampled at peak biomass at Contra-Costa in 2004 and 2005.

Effect	Herbage Component			
	Grass	Forb	*E. palustris*	Total
	----------------------------*P* Value----------------------------			
Above ground Biomass				
2002 Pre-flooding (Covariate)	0.86	0.83	**0.0001**	
Flooding Treatment	**0.009**	0.30	0.56	
Topographic Position	**<0.0001**	**0.009**	**0.05**	
Flooding x Position	**0.11***	0.73	**0.10**	
Sampling Year	**0.0006**	0.40	0.38	
Flooding x Year	0.78	0.15	0.55	
Position x Year	**0.06**	0.62	0.71	
Flooding x Position x Year	0.76	0.83	0.59	
Crude Protein (CP)				
2002 Pre-flooding (Covariate)	**0.07**	0.89	**0.0005**	
Flooding Treatment	**0.10**	0.25	0.42	
Topographic Position	**0.002**	**0.03**	**0.02**	
Flooding x Position	0.18	0.65	0.17	
Sampling Year	**0.07**	0.44	0.73	
Flooding x Year	0.75	0.24	0.71	
Position x Year	**0.01**	0.40	0.94	
Flooding x Position x Year	0.51	0.76	0.82	
Crude Protein Yield (CPY)				
2002 Pre-flooding (Covariate)	0.89	0.69	**0.0004**	0.43
Flooding Treatment	**0.006**	0.42	0.66	0.80
Topographic Position	**0.0001**	**0.11***	**0.07**	0.29
Flooding x Position	**0.03**	0.69	**0.09**	0.31
Sampling Year	**0.0004**	0.45	0.51	**0.009**
Flooding x Year	0.80	0.23	0.52	0.22
Position x Year	0.12	0.52	0.82	**0.04**
Flooding x Position x Year	0.81	0.57	0.44	0.19
Acid Detergent Fiber (ADF)				
2002 Pre-flooding (Covariate)	**0.02**	0.19	0.37	
Flooding Treatment	**0.02**	0.47	0.65	
Topographic Position	0.75	0.39	0.98	
Flooding x Position	0.32	0.43	0.81	
Sampling Year	0.55	0.17	0.23	
Flooding x Year	**0.05**	0.92	0.90	
Position x Year	0.70	0.90	0.96	
Flooding x Position x Year	**0.03**	0.89	.	

* considered significant at $P = 0.11$

Table 5.2: Landscape variation in above ground biomass and crude protein yield (CPY) of grass and *E. palustris* in response to three flooding treatments at Contra-Costa. Within a response variable, interaction means with different lowercase letters differ ($P < 0.05$). For the grass component, grand (flooding treatment) means of biomass and CPY with different uppercase letters differ ($P < 0.05$).

Component	Position	Biomass (g m^{-2})			Crude Protein Yield (g m^{-2})		
		FF[1]	SF	NF	FF[1]	SF	NF
Grass	Upland	340.2 a	195.1 c	171.9 c	27.1 a	14.6 b	14.4 b
	Waterline	85.0 d	341.4 a	359.6 a	7.6 c	26.7 a	27.6 a
	Shallow Flooding	6.7 f	36.5 e	260.0 b	0.7 d	3.5 c	24.7 a
	Deep Flooding	1.5 f	0.4 f	35.9 e	0.4 d	0.0 d	4.2 c
	Mean (Flooding)	***108.3 B***	***143.3 B***	***206.8 A***	***9.0 B***	***11.2 B***	***17.7 A***
	(SE)		***(23.5)***			***(2.1)***	
E. palustris	Upland	32.7 c	32.7 c	32.7 c	5.8 c	5.8 c	5.8 c
	Waterline	298.4 a	32.7 c	32.7 c	29.9 a	5.8 c	5.8 c
	Shallow Flooding	171.8 b	300.1 a	133.1 b	17.0 b	37.2 a	13.2 b
	Deep Flooding	153.8 b	316.9 a	252.6 a	16.6 b	26.0 a	26.9 a
	(SE)		***(32.5)***			***(3.5)***	

[1] FF, SF and NF represent Fall Flooding, Spring Flooding and Natural Flooding treatments, respectively.

Table 5.3: Variation in above ground grass biomass (g m^{-2}), crude protein (%) and crude protein yield (g m^{-2}) across topographic positions at Contra-Costa in 2004 and 2005. Within a response variable, interaction means with different lowercase letters differ ($P < 0.05$) and grand (annual) means with different uppercase letters differ ($P < 0.05$).

Topographic Position	Grass Biomass		Grass Crude Protein		Grass Crude Protein Yield	
	2004	2005	2004	2005	2004	2005
Upland	143.9 b	327.6 a	8.6 a	8.6 a	11.7	25.7
Waterline	148.2 b	375.7 a	7.4 ab	6.6 b	13.3	28.0
Shallow Flooding	66.2 c	135.8 b	1.4 c	7.8 ab	6.2	13.0
Deep Flooding	11.9 d	13.3 d	1.3 c	1.5 c	1.7	1.4
Mean (Year)	***92.6 B***	***213.1 A***	***(4.7) B***	***(6.1) A***	***8.2 B***	***17.0 A***
(SE)	***(42.6)***		***(0.5)***		***(3.1)***	

Table 5.4: Landscape variation in above ground biomass, crude protein (CP) and crude protein yield (CPY) of grass, forb and *E. palustris* at Contra-Costa. Within a response variable and herbage component, position means with different lowercase letters differ ($P < 0.05$).

Variable	Position	Grass	*(SE)*	Forb	*(SE)*	*E. palustris*	*(SE)*
Biomass (gm^{-2})	Upland	235.8 a	*(50.7)*	17.3 a	*(0.8)*	32.7 c	*(40.0)*
	Waterline	262.0 a		17.4 a		121.2 b	
	Shallow Flooding	101.0 b		2.9 b		201.7 a	
	Deep Flooding	12.6 c		0.4 c		241.1 a	
CP (%)	Upland	8.6 a	*(1.4)*	6.6 a	*(1.6)*	2.2 b	*(1.3)*
	Waterline	7.0 a		8.7 a		3.8 b	
	Shallow Flooding	4.6 b		2.5 b		7.8 a	
	Deep Flooding	1.4 c		1.4 b		5.9 a	
CPY (g m^{-2})	Upland	18.7 a	*(3.8)*	1.5 b	*(0.1)*	5.8 c	*(3.5)*
	Waterline	20.6 a		2.1 a		13.8 b	
	Shallow Flooding	9.6 b		0.3 c		22.5 a	
	Deep Flooding	1.5 c		0.1 c		23.2 a	

Table 5.5: Spatial and temporal variation in total crude protein yield (CPY) of all herbage components at Contra-Costa. Interaction means with different lowercase letters differ ($P < 0.05$). Grand means of sampling years differ ($P = 0.009$).

Topographic Position	Sampling Year	
	2004	2005
Upland	11.7 c	27.3 b
Waterline	27.1 b	39.6 a
Shallow Flooding	30.8 b	37.4 a
Deep Flooding	39.6 a	34.4 ab
Mean	***27.3 B***	***34.7 A***
(SE)	***(2.6)***	

Table 5.6: Variation in acid detergent fiber (ADF) (%) content of grass at Contra-Costa in response to three flooding treatments. Flooding treatment × sampling year means with different lowercase letters differ ($P < 0.05$). Flooding treatment (grand) means with different uppercase letters differ ($P < 0.05$).

Flooding Treatment	Topographic Position	Sampling Year		Mean (Flooding)
		2004	2005	
Fall Flooding	Upland	43.1	44.9	
	Waterline	48.7	39.6	
	Shallow Flooding	-	39.6	
	Mean	***45.9 a***	***41.4 c***	***43.7 A***
Spring Flooding	Upland	40.5	43.6	
	Waterline	37.6	42.4	
	Shallow Flooding	-	39.9	
	Mean	***39.1 d***	***42.0 bc***	***40.5 B***
Natural Flooding	Upland	43.9	40.9	
	Waterline	41.6	44.9	
	Shallow Flooding	44.0	46.4	
	Mean	***43.2 b***	***44.1 ab***	***43.6 A***
	(Pooled SE)	***(0.9)***		

Table 5.7: Summary of statistical tests indicating *P*-values on the effects of flooding treatment and depth (topographic position), as well as the presence of cattle grazing, on above ground biomass, crude protein concentration, crude protein yield and acid detergent fiber of grass, forb, *E. palustris* and *T. latifolia* at Kitsim. Sampling occurred at peak biomass at the end of each flooding treatment (2004) and after subsequent reflooding (2005) in established wetlands.

	Herbage Component							
Effect	Grass		Forb		*E. palustris*		*T. latifolia*	
	2004	2005	2004	2005	2004	2005	2004	2005
	----------*P* Value----------							
Biomass								
Flooding (F)	**0.06**	**0.10**	**0.004**	**0.06**	**0.05**	**0.11***	**<0.0001**	**0.003**
Position (P)	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.009**	**0.006**	**<0.0001**	**<0.0001**
F x P	0.48	**0.07**	**0.0007**	**0.06**	0.30	0.38	**<0.0001**	**0.002**
Grazing (G)	**<0.0001**	**0.01**	**<0.0001**	**0.10**	0.24	**0.05**	0.16	0.27
G x F	0.24	**0.07**	0.19	0.68	**0.002**	0.52	0.53	0.25
G x P	0.13	0.51	**0.009**	0.96	0.85	0.68	**0.11***	**0.10**
G x P x F	0.79	0.66	0.50	0.63	0.19	0.13	0.56	0.80
CP								
Flooding (F)	0.28	0.70	**0.01**	0.27	0.42	0.53	**0.07**	0.21
Position (P)	0.14	**0.0003**	**0.03**	**0.02**	0.88	0.15	0.57	0.31
F x P	0.92	0.63	0.18	0.83	0.58	0.88	0.65	0.70
Grazing (G)	-	0.66	-	**0.05**	-	0.41	-	0.90
G x F	-	0.16	-	0.38	-	0.57	-	0.31
G x P	-	**0.06**	-	0.97	-	0.16	-	0.56
G x P x F	-	0.30	-	0.99	-	.	-	0.84
CPY								
Flooding (F)	0.14	**0.02**	0.62	0.60	0.56	**0.03**	0.60	**0.004**
Position (P)	0.43	**0.10**	**0.02**	**0.11**	**0.009**	**0.004**	0.44	0.27
F x P	0.70	**0.03**	0.68	0.31	0.69	0.60	0.66	0.96
Grazing (G)	-	**0.04**	-	0.28	-	0.65	-	0.25
G x F	-	**0.04**	-	0.27	-	0.87	-	0.21
G x P	-	0.75	-	0.36	-	0.76	-	0.51
G x P x F	-	0.61	-	0.94	-	0.21	-	0.15
ADF								
Flooding (F)	0.55	**0.008**	0.31	**0.09**	0.99	0.23	0.48	**0.05**
Position (P)	0.91	**0.05**	**0.006**	**<0.0001**	0.83	0.35	0.36	**0.11***
F x P	0.55	0.91	0.38	0.75	0.70	0.74	0.30	0.95
Grazing (G)	-	0.21	-	0.67	-	0.63	-	0.83
G x F	-	0.42	-	0.80	-	0.20	-	0.86
G x P	-	0.85	-	0.35	-	**0.10**	-	0.92
G x P x F	-	0.59	-	0.89	-	.	-	0.90

'-' indicates hypothesis testing did not include the interaction with cattle grazing.
* considered significant at $P = 0.11$.

Table 5.8: Landscape variation in above ground biomass (g m^{-2}) of (A) grass and (B) forb in response to four flooding treatments, sampled at the end of flooding treatment (2004) and post reflooding (2005) at Kitsim. Within herbage component and sampling period, flooding × position interaction means with different lowercase letters differ ($P < 0.05$). Grand means of flooding treatment or topographic positions with different uppercase letters differ ($P < 0.05$).

(A) Grass Biomass

Topographic Position	End of Flooding (2004)					Post Reflooding (2005)				
	FF[1]	SF	1YNF	2YNF	***Mean (Position)***	FF	SF	1YNF	2YNF	***Mean (Position)***
Upland	150.8	132.8	145.2	112.9	***135.4 A***	204.9 c	241.8 bc	239.1 bc	244.0 bc	***232.5 A***
Dry Meadow	159.0	191.9	79.7	131.3	***140.5 A***	149.3 d	314.8 a	276.0 ab	199.2 c	***234.8 A***
Wet Meadow	37.6	143.2	7.5	17.3	***51.4 B***	97.7 e	282.8 ab	69.9 e	28.0 f	***119.6 B***
Deep Marsh	0.0	8.5	1.5	3.0	***3.3 C***	1.5 g	1.9 g	1.6 g	26.2 f	***7.8 C***
Mean (Flooding)	***86.9 B***	***119.1 A***	***58.5 C***	***66.1 C***		***113.4 B***	***210.3 A***	***146.7 B***	***124.3 B***	
(SE)			***(11.7)***					***(18.8)***		

(B) Forb Biomass

Topographic Position	End of Flooding (2004)					Post Reflooding (2005)				
	FF[1]	SF	1YNF	2YNF	***Mean (Position)***	FF	SF	1YNF	2YNF	***Mean (Position)***
Upland	11.2 ef	7.0 f	4.6 f	5.0 f	***7.0 C***	22.6 e	15.4 e	14.5 e	9.9 ef	***15.6 C***
Dry Meadow	97.7 b	37.3 d	49.0 d	36.3 d	***55.1 B***	71.2 cd	92.0 bc	97.0 bc	82.2 c	***85.6 A***
Wet Meadow	17.7 e	62.7 cd	78.0 bc	177.0 a	***83.8 A***	21.5 e	100.5 bc	52.1 d	144.1 a	***79.5 A***
Deep Marsh	0.0 g	5.0 f	53.2 cd	170.1 a	***57.1 B***	7.7 f	0.0 f	1.7 f	108.7 b	***29.5 B***
Mean (Flooding)	***31.6 B***	***28.0 B***	***46.2 B***	***97.1 A***		***30.7 C***	***52.0 B***	***41.3 BC***	***86.2 A***	
(SE)			***(13.8)***					***(10.4)***		

[1] FF, SF, 1YNF and 2YNF treatments represent Fall Flooding, Spring Flooding, One Year of No Flooding, and Two Years of No Flooding, respectively.

Table 5.8 (cont'd): Landscape variation in above ground biomass (g m^{-2}) of (C) *E. palustris* and (D) *T. latifolia* in response to four flooding treatments, sampled at the end of flooding treatment (2004) and post reflooding (2005) at Kitsim. Within a herbage component and sampling period, flooding × position interaction means with different lowercase letters differ ($P < 0.05$). Grand means of flooding treatment or topographic positions with different uppercase letters differ ($P < 0.05$).

(C) *E. palustris* Biomass

Topographic Position	End of Flooding (2004)					Post Reflooding (2005)				
	FF[1]	SF	1YNF	2YNF	***Mean (Position)***	FF	SF	1YNF	2YNF	***Mean (Position)***
Upland	0.0	0.0	0.0	0.0	***0.0 C***	0.0	0.0	0.0	0.0	***0.0 C***
Dry Meadow	0.0	0.0	0.3	0.0	***0.1 C***	0.3	1.5	0.0	0.0	***0.4 C***
Wet Meadow	8.3	5.4	18.1	0.0	***8.0 B***	8.5	25.9	36.0	4.4	***18.7 A***
Deep Marsh	0.0	22.9	34.1	0.0	***14.3 A***	0.0	0.4	49.8	0.0	***12.6 B***
Mean (Flooding)	***2.1 C***	***7.1 B***	***13.1 A***	***0.0 D***		***2.2 C***	***6.9 B***	***21.5 A***	***1.1 C***	
(SE)			***(2.5)***					***(4.1)***		

(D) *T. latifolia* Biomass

Topographic Position	End of Flooding (2004)					Post Reflooding (2005)				
	FF[1]	SF	1YNF	2YNF	***Mean (Position)***	FF	SF	1YNF	2YNF	***Mean (Position)***
Upland	0.0 f	0.0 f	0.0 f	0.0 f	***0.0 C***	0.0 f	0.0 f	0.0 f	0.0 f	***0.0 C***
Dry Meadow	0.9 f	1.3 f	1.6 f	0.0 f	***0.9 C***	0.0 f	0.0 f	0.3 f	0.7 f	***0.2 C***
Wet Meadow	85.6 c	7.7 e	5.0 e	0.2 f	***24.6 B***	142.6 c	82.0 d	56.3 de	28.3 e	***77.3 B***
Deep Marsh	696.5 a	335.5 b	103.7 c	34.8 d	***292.6 A***	478.2 b	799.0 a	179.6 c	54.1 de	***377.7 A***
Mean (Flooding)	***195.7 A***	***86.1 B***	***27.6 C***	***8.7 D***		***155.2 B***	***220.2 A***	***59.0 C***	***20.8 D***	
(SE)			***(36.5)***					***(39.3)***		

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[1] FF, SF, 1YNF and 2YNF treatments represent Fall Flooding, Spring Flooding, One Year of No Flooding, and Two Years of No Flooding, respectively.

Table 5.9: Variation in above ground grass biomass (g m^{-2}) under four flooding regimes between ungrazed and grazed sites at the end of flooding treatment (2004) and post reflooding (2005) at Kitsim. Within a sampling period, flooding × grazing interaction means with different lowercase letters differ ($P < 0.05$), and grand means of grazing treatments with different uppercase letters differ ($P < 0.01$).

Grazing Treatment	End of Flooding (2004)					Post Reflooding (2005)				
	FF[1]	SF	1YNF	2YNF	***Mean (Grazing)***	FF	SF	1YNF	2YNF	***Mean (Grazing)***
Ungrazed	68.6	157.1	59.2	73.4	***89.6 A***	71.7 c	167.1 a	70.0 c	97.6 b	***101.6 B***
Grazed	52.2	57.8	22.8	29.4	***40.6 B***	107.3 b	164.4 a	155.9 a	103.9 b	***132.8 A***
(SE)		***(13.6)***					***(13.2)***			

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[1] FF, SF, 1YNF and 2YNF treatments represent Fall Flooding, Spring Flooding, One Year of No Flooding, and Two Years of No Flooding, respectively.

Table 5.10: Landscape variation in above ground biomass (g m^{-2}) of forbs between grazed and ungrazed sites sampled at the end of flooding treatment (2004) and post reflooding (2005) at Kitsim. Within a sampling period, grazing × position interaction means with different lowercase letters differ ($P < 0.05$). Grand (ungrazed vs. grazed) means with different uppercase letters differ ($P < 0.05$).

Topographic	End of Flooding (2004)		Post Reflooding (2005)	
Position	Ungrazed	Grazed	Ungrazed	Grazed
Upland	9.1 d	4.7 d	13.7	16.9
Dry Meadow	80.1 b	30.9 c	74.5	96.8
Wet Meadow	138.7 a	28.6 c	63.2	80.8
Deep Marsh	40.8 c	24.7 c	9.9	16.9
Mean	***67.2 A***	***22.2 B***	***40.3 B***	***52.8 A***
(SE)	*(15.9)*		*(4.4)*	

Table 5.11: Variation in above ground *E. palustris* biomass (g m^{-2}) under four flooding treatments between grazed and ungrazed sites at end of flooding treatment (2004) and post reflooding (2005) at Kitsim. Within a sampling period, interaction means with different uppercase letters differ ($P < 0.05$). Grand (ungrazed vs. grazed) means with different uppercase letters differ ($P < 0.05$).

Flooding Treatment	2004		2005	
	Ungrazed	Grazed	Ungrazed	Grazed
FF[1]	0.8 cd	0.4 d	0.5	1.3
SF	1.3 c	5.9 b	2.8	3.3
1YNF	16.9 a	1.5 c	5.4	17.7
2YNF	0.0 e	0.0 e	0.0	1.1
Mean	***4.8***	***1.9***	***2.2 B***	***5.8 A***
(SE)	***(1.0)***		***(1.3)***	

[1] FF, SF, 1YNF and 2YNF treatments represent Fall Flooding, Spring Flooding, One Year of No Flooding, and Two Years of No Flooding, respectively.

Table 5.12: Landscape variation in above ground biomass (g m^{-2}) of *T. latifolia* between grazed and ungrazed sites sampled at the end of flooding treatment (2004) and post reflooding (2005) at Kitsim . Within a sampling period, grazing × position interaction means with different lowercase letters differ ($P < 0.05$).

Topographic Position	End of Flooding (2004)		Post Reflooding (2005)	
	Ungrazed	Grazed	Ungrazed	Grazed
Upland	0.0 d	0.0 d	0.0 e	0.0 e
Dry Meadow	1.5 d	0.2 d	0.2 e	0.1 e
Wet Meadow	11.6 c	15.5 c	45.6 d	103.1 c
Deep Marsh	292.6 a	176.6 b	302.9 b	325.6 a
(SE)	*(10.0)*		*(7.1)*	

Table 5.13: Landscape variation in crude protein concentration (%) of forb in response to four flooding treatments, sampled at the end of flooding treatment (2004) and post reflooding (2005) at Kitsim. Grand means of flooding treatment and topographic positions with different uppercase letters differ ($P < 0.05$).

Topographic Position	End of Flooding (2004)					Post Reflooding (2005)				
	FF[1]	SF	1YNF	2YNF	***Mean (Position)***	FF	SF	1YNF	2YNF	***Mean (Position)***
Upland	8.9	11.4	10.4	9.8	***10.1 B***	9.8	10.5	10.7	11.7	***10.7 A***
Dry Meadow	9.3	10.0	15.4	10.6	***11.3 B***	9.4	9.1	11.6	9.7	***10.0 B***
Wet Meadow	11.4	11.2	11.6	7.9	***10.5 B***	10.3	7.9	11.1	9.7	***9.7 B***
Deep Marsh	16.7	12.1	18.1	9.4	***14.1 A***	6.9		7.0	7.0	***7.0 C***
Mean (Flooding)	***11.5 B***	***11.2 B***	***13.9 A***	***9.4 C***		***9.1***	***9.2***	***10.1***	***9.6***	
(SE)			***(0.8)***					***(0.2)***		

[1] FF, SF, 1YNF and 2YNF treatments represent Fall Flooding, Spring Flooding, One Year of No Flooding, and Two Years of No Flooding, respectively.

Table 5.14: Variation in grass crude protein yield (g m^{-2}) across (A) topographic positions and (B) grazing treatments under four flooding treatments at Kitsim during post reflooding sampling in 2005. Interaction means with different lowercase letters differ ($P < 0.05$). Grand means with different uppercase letters differ ($P < 0.05$).

(A)

Topographic Position	Flooding Treatment				***Mean***
	FF[1]	SF	1YNF	2YNF	***(Position)***
Upland	27.1 cd	24.4 cd	27.1 cd	31.9 c	***27.6 A***
Dry Meadow	16.6 e	38.3 b	27.6 cd	15.7 e	***24.6 A***
Wet Meadow	22.9 d	45.6 a	27.6 cd	5.9 f	***25.5 A***
Deep marsh		9.9 f		8.2 f	***9.1 B***
Mean (Flooding)	***22.2 AB***	***29.6 A***	***27.5 A***	***15.4 B***	
(SE)		***(2.7)***			

(B)

Topographic Position	Flooding Treatment				***Mean***
	FF[1]	SF	1YNF	2YNF	***(Grazing)***
Ungrazed	19.2 cd	26.7 b	18.6 cd	15.7 d	**20.1 B**
Grazed	25.2 bc	32.6 ab	36.3 a	15.2 d	**27.3 A**
Mean (Flooding)	***22.2 AB***	***29.6 A***	***27.5 A***	***15.4 B***	
(SE)		***(2.7)***			

[1] FF, SF, 1YNF and 2YNF treatments represent Fall Flooding, Spring Flooding, One Year of No Flooding, and Two Years of No Flooding, respectively.

Table 5.15: Landscape variation in crude protein yield (g m^{-2}) of forb in 2004 and 2005 at Kitsim. Within a sampling year, topographic position means with different lowercase letters differ ($P < 0.05$).

Topographic Position	Sampling Year	
	2004	2005
Upland	1.8 c	7.4 b
Dry Meadow	11.6 b	13.0 a
Wet Meadow	13.2 ab	14.6 a
Deep marsh	17.9 a	11.6 a
(SE)	***(2.9)***	***(1.3)***

Table 5.16: Landscape variation in total herbage crude protein yield (g m^{-2}) in response to four flooding treatments, sampled after reflooding in 2005 at Kitsim. Flooding treatment × topographic position means with different lowercase letters differ ($P < 0.05$). Grand means of flooding treatment and topographic positions with different uppercase letters differ ($P < 0.05$).

Topographic Position	Flooding Treatment				***Mean (Position)***
	FF[1]	SF	1YNF	2YNF	
Upland	38.7 d	29.1 e	31.3 de	37.0 de	***34.0 C***
Dry Meadow	26.1 e	46.4 c	43.5 cd	26.7 e	***35.7 C***
Wet Meadow	66.7 b	94.1 a	62.5 b	41.0 d	***66.1 A***
Deep marsh	51.1 c	53.0 c	55.1 bc	26.5 e	***46.4 B***
Mean (Flooding)	***45.7 A***	***55.7 A***	***48.1 A***	***32.8 B***	
(SE)		***(4.1)***			

[1] FF, SF, 1YNF and 2YNF treatments represent Fall Flooding, Spring Flooding, One Year of No Flooding, and Two Years of No Flooding, respectively.

Table 5.17: Landscape variation in acid detergent fiber content (%) of (A) grass, (B) forb, and (C) *T. latifolia* in response to four flooding treatments, sampled after reflooding in 2005 at Kitsim. Within a herbage component, grand means of flooding treatment and topographic position with different uppercase letters differ ($P < 0.05$).

(A) Grass ADF

Topographic Position	Flooding Treatment				***Mean (Position)***
	FF[1]	SF	1YNF	2YNF	
Upland	40.0	42.8	42.4	42.6	***41.9 B***
Dry Meadow	41.0	44.6	45.5	43.4	***43.6 AB***
Wet Meadow	42.4	44.9	44.0	43.3	***43.6 AB***
Deep marsh	-	-	-	45.1	***45.1 A***
Mean (Flooding)	***41.1 B***	***44.1 A***	***44.0 A***	***43.6 A***	
(SE)	***(0.6)***				

(B) Forb ADF

Topographic Position	Flooding Treatment				***Mean (Position)***
	FF[1]	SF	1YNF	2YNF	
Upland	42.9	39.6	40.8	39.2	***40.6 C***
Dry Meadow	36.1	34.6	41.1	36.7	***37.1 C***
Wet Meadow	46.5	47.1	48.3	44.3	***46.6 B***
Deep marsh	55.1		58.4	50.7	***54.7 A***
Mean (Flooding)	***45.1 A***	***40.4 B***	***47.2 A***	***42.7 B***	
(SE)	***(1.3)***				

(C) *T. latifolia* ADF

Topographic Position	Flooding Treatment				***Mean (Position)***
	FF[1]	SF	1YNF	2YNF	
Upland	-	-	-	-	-
Dry Meadow	-	-	-	-	-
Wet Meadow	46.0	44.7	44.4	40.6	***43.9 B***
Deep marsh	46.7	47.4	46.0	41.5	***45.4 A***
Mean (Flooding)	***46.4 A***	***46.0 A***	***45.2 A***	***41.0 B***	
(SE)	***(1.1)***				

[1] FF, SF, 1YNF and 2YNF treatments represent Fall Flooding, Spring Flooding, One Year of No Flooding, and Two Years of No Flooding, respectively.

Table 5.18: Landscape variation in (A) absolute and (B) relative herbage utilization across landscapes under three flooding treatments at Contra-Costa, as sampled in October 2005. Within a response variable, grand means of flooding treatment and topographic position with different uppercase letters differ ($P < 0.05$).

(A) Absolute Utilization (g m^{-2})

Topographic Position	Flooding Treatment			***Mean (Position)***
	NF[1]	FF	SF	
Upland	0.5	37.4	25.5	***20.8 B***
Waterline	17.8	36.4	49.9	***34.7 B***
Shallow Flooding	23.2	85.2	75.5	***61.3 A***
Deep Flooding	5.2	61.4	-	***33.3 B***
Mean (Flooding)	***11.4 B***	***55.1 A***	***50.3 A***	
(SE)		***(11.3)***		

(B) Relative Utilization (%)

Topographic Position	Flooding Treatment			***Mean (Position)***
	NF[1]	FF	SF	
Upland	1.8	21.6	36.8	***20.1 B***
Waterline	10.2	20.4	26.3	***19.0 B***
Shallow Flooding	8.5	53.7	44.2	***35.5 A***
Deep Flooding	3.5	22.9	-	***13.2 B***
Mean (Flooding)	***6.0 B***	***29.6 A***	***35.8 A***	
(SE)		***(7.4)***		

[1] NF, FF and SF treatments represent Natural Flooding, Fall Flooding, and Spring Flooding, respectively.

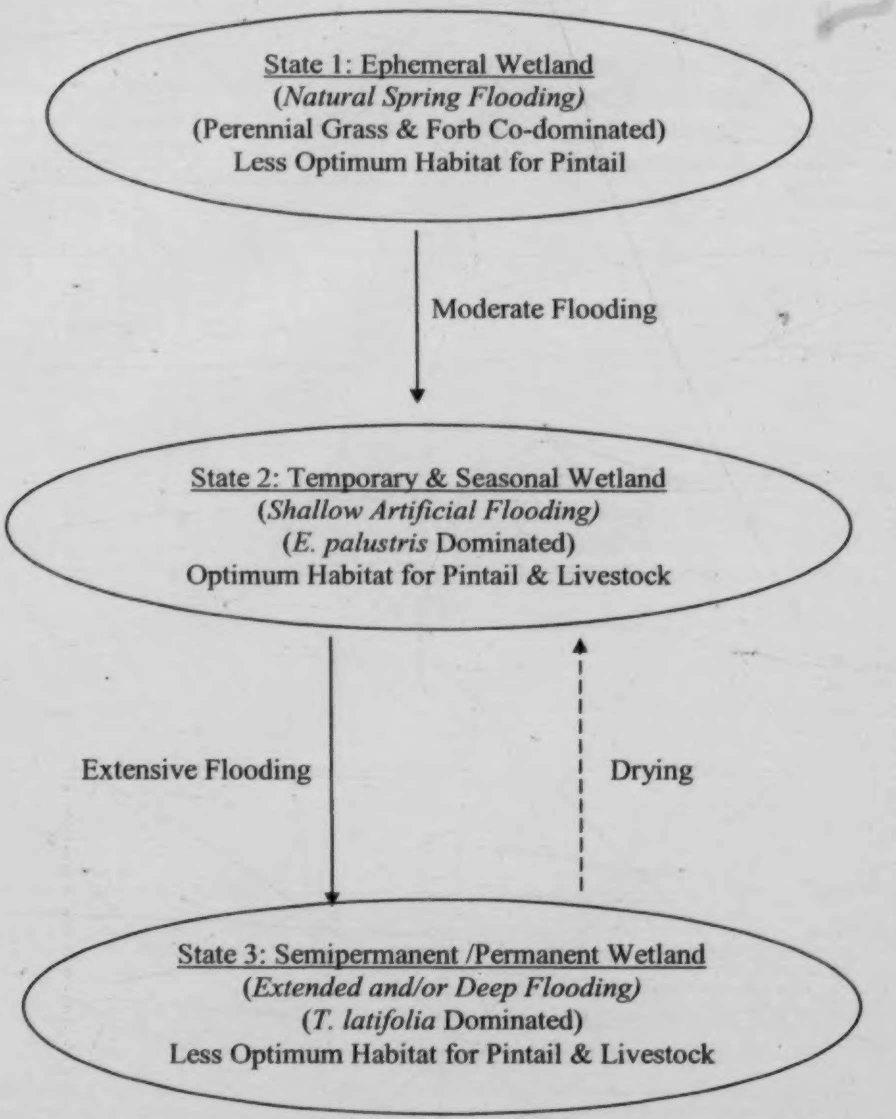
State 1: Ephemeral Wetland
(*Natural Spring Flooding)*
(Perennial Grass & Forb Co-dominated)
Less Optimum Habitat for Pintail
Moderate Flooding
State 2: Temporary & Seasonal Wetland
(*Shallow Artificial Flooding)*
(*E. palustris* Dominated)
Optimum Habitat for Pintail & Livestock
Extensive Flooding
Drying
State 3: Semipermanent /Permanent Wetland
(*Extended and/or Deep Flooding)*
(*T. latifolia* Dominated)
Less Optimum Habitat for Pintail & Livestock

Fig. 5.1: Theorized model of vegetation succession following wetland creation in the Dry Mixed Grass Prairie of southeastern Alberta, Canada. State 2 constitutes the desired plant community (DPC) that provides the habitat mosaic optimum for Northern Pintail and rangeland cattle. While moderate and extensive flooding of newly created wetlands may facilitate succession to states 2 and 3, respectively, wetland drying may facilitate community change from state 3 to 2 (the DPC).

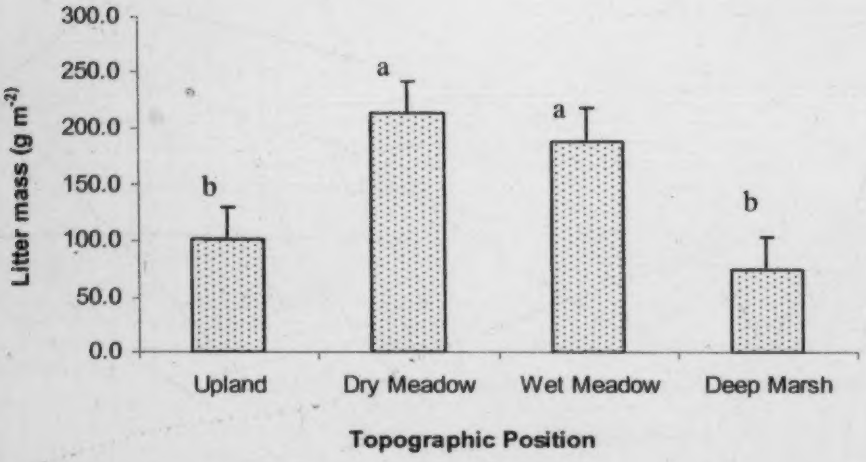

Fig. 5.2: Spatial distribution of mean litter mass (+ SE) across topographic positions at Kitsim, as sampled in 2005. Position means with different lowercase letters differ ($P < 0.05$).

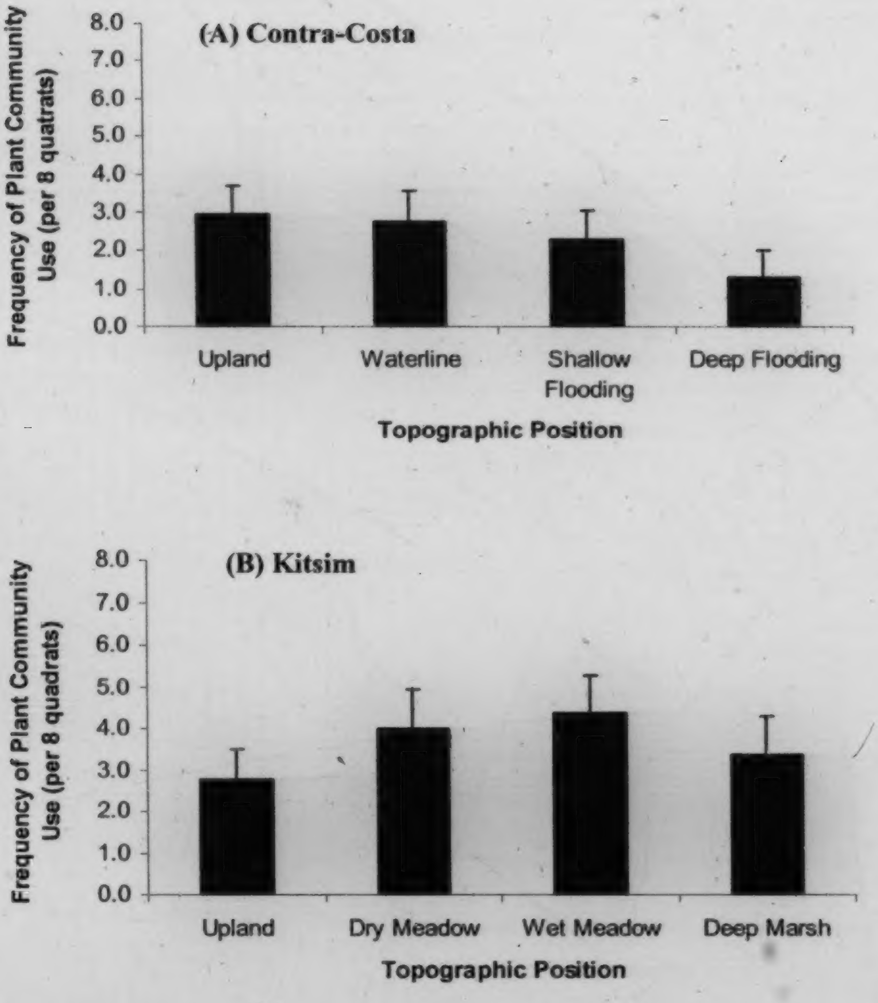

Fig. 5.3: Spatial trends in plant community use by cattle across topographic positions at (A) Contra-Costa and (B) Kitsim, as sampled in August 2004.

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CHAPTER 6

FLOOD SEASONALITY AND FREQUENCY EFFECTS ON THE ABUNDANCE OF NORTHERN PINTAIL AND THEIR HABITAT IN THE DRY MIXED GRASS PRAIRIE

6.1. Introduction

The Prairie Pothole Region (PPR) of Canada has been described as the "duck factory" of North America, where many waterfowl species breed each year (Krapu 2000). Climatic and anthropogenic factors have accounted for regional declines in breeding waterfowl abundance during the last few decades (Dickson 1989, Caithamer et al. 1992). In particular, current breeding populations of Northern Pintail (*Anas acuta*) (Appendix XVIII), American Wigeon (*Anas Americana*), Mallard (*Anas platyrhynchos*) and Lesser Scaup (*Aytha affinis*) are well below the population management goals of the North American Waterfowl Management Plan (NAWMP) agreement (Wilkins and Otto 2006).

Waterfowl habitats in the PPR are under serious threat from intensified agriculture (Boyd 1985, Millar 1989, Nudds and Clark 1993, Miller and Duncan 1999, Podruzny et al. 2002), drought (Johnson and Grier 1988, Williams et al. 1999, Nudds 1983) and wetland drainage (Millar 1989, Nudds and Clark 1993, Podruzny et al. 2002). Collectively, these factors have accounted for the loss of prairie wetlands and suitable upland nesting habitats (Johnson and Grier 1988, Turner et al. 1987). Waterfowl management in the PPR has therefore embarked on efforts to secure less disturbed landscapes through conservation easements, and subsequently manage these landscapes to restore and enhance waterfowl habitats (Krapu et al. 1997, Bethke and Nudds 1995).

Habitat management for breeding waterfowl involves manipulations that preserve, add, or modify habitats to influence recruitment or survival rates (Koeln et al. 1996). The most difficult decision confronting waterfowl managers is selecting habitat manipulations that, alone or in combination, will have the desired effect on waterfowl productivity (Koeln et al. 1996, Koper and Schmiegelow 2006a). Annual recruitment is ultimately associated with reproductive success for many species of waterfowl, as affected by population parameters and both habitat availability and quality (Koeln et al. 1996, Koper and Schmiegelow 2006b). The temporal cue that triggers egg-laying is related to ambient temperatures during spring, with nest initiation occurring earlier when spring temperatures are warmer (Langford and Driver 1979, Krapu and Doty 1979, Fredga and Dow 1983, Greenwood et al. 1995). Ambient temperature also influences food availability, which altogether affect the timing of nest initiation (Krapu and Reinecke 1992, Krapu 2000). Furthermore, food availability is influenced by the frequency and amount of precipitation (Bataille and Baldassarre 1993), as well as the fluctuating levels of water in wetlands (Braithwaite and Frith 1969). In addition, cattle grazing adversely impact the abundance of certain wetland invertebrates through reduction in vegetation structure (Foote and Hornung 2005). Meanwhile, vegetation richness has been shown to correlate positively with that of wetland invertebarates such as odonates in the PPR (Hornung and Rice 2003).

The Northern Pintail (*aka.* Pintail) is a typical prairie breeding duck of management concern in southwestern Canada (Austin and Miller 1995). It is among the first migrant waterfowl to arrive after snow-melt in spring, and promptly responds to favorable wetland conditions by initiating breeding and nesting activities (Austin and Miller 1995). Being an early nester, Pintails often encounter light snowfall during egg-laying and incubation (Bellrose 1980). Compared to other dabbling ducks, Pintails have limited capacity to re-nest during late spring, and this is a critical factor affecting their long-term population declines in the prairies (Austin and Miller 1995, Krapu et al. 2002). Typical nesting landscapes include open short prairie grasslands interspersed with shallow, seasonal and semipermanent wetlands (Kaminski and Weller 1992). These habitats were historically abundant in the PPR, and held the greatest populations of breeding Northern Pintails in the continent (Austin and Miller 1995). Stewart and Kantrud (1973) indicated that in North Dakota, 40% of Pintail breeding pairs were found on seasonal wetlands, 24% on cultivated "temporary" wetland basins, 19% on semi-permanent wetlands, with very few on permanent wetlands, streams, reservoirs or large impoundments. Stewart and Kantrud (1974) further indicated that breeding pair density was positively correlated with wetland size, as well as the abundance of seasonal and semi-permanent wetlands across the landscape. Breeding pair densities were also influenced by the degree of interspersion of emergent plant cover and open water within available wetlands (Kaminski and Prince 1984).

In 1983, Ducks Unlimited Canada (DUC), under agreements with local irrigation administrations and landowners, created semi-permanent and permanent wetlands for enhancing waterfowl production in the Dry Mixed Grass Prairie (DMP) of southeastern Alberta, Canada (Sankowski et al. 1987). DUC's primary goal was to stop the population decline of Pintails through habitat enhancement, and restore their numbers to population goals defined by the North American Waterfowl Management Plan (Appendix XVIII) (NAWMP 1986). These wetlands were created and maintained by artificial flooding to augment the available moisture in naturally occurring meadows originally dominated by native plant communities such as hydric grasses, sedges and forbs. Selected wetlands were originally flooded three times a year between May and August to maintain permanence (Dave Kay *pers. comm.*), which initially resulted in greater spikerush (*Eleocharis palustris*) production, as well as increased use and productivity among Pintail and other waterfowl within these landscapes (Sankowski et al. 1987). Although there is no record of direct Pintail use as food, *E. palustris* is a typical plant species characteristic of seasonal wetlands preferred by Pintail in the DMP. The maintenance of permanent wetlands altered wetland vegetation composition and structure by facilitating invasion of cattail (*Typha latifolia*) and displacement of *E. palustris* (Dave Kay *pers. comm.*).

In early 2000, flooding regimes changed to once a year in August / September (i.e., fall) to reduce wetland permanence, with the hope of restoring low structured, more open habitats preferred by Pintails. While fall flooding may not coincide with the predominantly spring-based historical flooding regime present in the region, this practice was necessary due to greater water availability in fall following declines in the demand for irrigation agriculture. To date, little information is available on the comparative effects of flooding seasonality on the use of these created wetlands by Pintail and other waterfowl, nor on the associated habitat quality, specifically structure and cover, within these managed landscapes. This information is needed for newly created wetlands, as well as older, established wetlands where vegetation changes have progressed beyond the desired plant community (Fig. 6.1). In the latter situation, reductions in flooding frequency may be necessary to reverse previous vegetation development to *T. latifolia*, and restore a more open wetland condition.

Combined, this information would help regional waterfowl managers make informed decisions about the optimal anthropogenic flood regimes required to maximize

Pintail production. According to Frederickson and Heitmeyer (1991), gradual flooding and subsequent natural drying of seasonal /semi-permanent wetlands during spring and summer, respectively, may create conditions optimal for the production of chironomids and other macroinvertebrates used as food by Pintail and other ducks in the PPR.

To explore the effect of wetland flooding treatments on the abundance of Pintail and 'Other Waterfowl', as well as the associated habitat availability, field-based studies were implemented at two wetland development sites, including within newly flooded wetlands at Contra-Costa, and within older, established wetlands at the Kitsim complex in the DMP. Habitat structure (maximum community height) and vegetation density (visual obstruction) were measured to understand the effects of flooding treatments on the potential use of these indices as predictors of site productivity (Robel et al. 1970) and waterfowl nesting habitat suitability (Higgins and Baker 1982).

6.2. Materials and Methods

6.2.1. Description of Study Sites

Both Contra-Costa and Kitsim are located near the city of Brooks (50° 33' N; 111° 51' W) in the DMP of southeastern Alberta, Canada. Brooks is an agricultural settlement, relying on irrigation water for primary production. While much of the landscape has been tilled, many native rangelands remain that are used for cattle grazing, wildlife habitat conservation, recreation and energy extraction. DUC's management in the region includes the maintenance and regulation of a series of anthropogenically flooded wetland complexes. Wetlands are flooded using gravity-fed irrigation canal systems that transport water from holding reservoirs. Using strategically-placed flood control structures, DUC is capable of regulating the timing (i.e., season) and amount (i.e., depth) of flooding in adjacent wetlands. In addition to artificial flooding, wetland moisture is affected by annual recharge from spring snow melt and growing season rainfall, as well as year-round losses due to evapotranspiration. Average long-term (30-year) and growing season precipitation and temperature during the study from 2001 to 2005 are provided in Appendices I and II, respectively (Environment Canada *unpubl.*).

A total of 8 and 16 wetlands were selected at the Contra-Costa and Kitsim complexes in August 2002, respectively. Wetlands at Contra-Costa were relatively new and comprised of minimally altered wet or dry meadow communities originally dominated by foxtail barley (*Hordeum jubatum* L.), western dock (*Rumex occidentalis* S. Wats.) and spikerush (*E. palustris*), while Kitsim wetlands were heavily dominated by *T. latifolia* following many years of extensive flooding.

6.2.2. Experimental Design and Flooding Treatments

A completely randomized design was used to assess the effects of different flooding treatments on the abundance of Pintail and other waterfowl at both Contra-Costa and Kitsim. Flooding treatments at Contra-Costa included annual fall flooding, spring flooding, and a control (no artificial flooding) (Appendix III). There were four replicates of fall flooded wetlands, while both spring and natural flooding were assigned only two. At Kitsim, flooding treatments included annual fall or spring flooding, as well as two flood cessation treatments (one versus two years of no artificial flooding, and a final reflood in fall 2004), with four replicate wetlands per treatment (Appendix IV).

A split-plot design within each wetland was used to assess the effects of individual flooding treatments on plant community structure and density, including maximum community height (MCH) and visual obstruction reading (VOR), respectively, at both Contra-Costa and Kitsim. Habitat structure and density were assessed within various topographic positions stratified across catena topo-sequences in the landscape. On new wetlands at Contra-Costa, the landscape was stratified into four depths of flooding, including deep flooding (60 cm), shallow flooding (30 cm), waterline (0 cm) and sub-irrigated upland (- 30 cm) zones. At Kitsim, where established wetlands had well-developed *T. latifolia* communities, both habitat structure and density were assessed in areas grazed and ungrazed by cattle. Under grazing disposition management of the Eastern Irrigation District, both Contra-Costa and Kitsim complexes were annually open to seasonal light to moderate cattle grazing from early summer (June) and mid fall (October). Cattle were prevented from grazing within 25 by 50 m exclosures built in 2003, which extended from the upland through to the deep marsh zone. Grazed and ungrazed areas were further stratified into deep marsh, wet meadow, dry meadow and upland zones for sampling. To evaluate flooding treatment effects on habitat structure and density, a 20-m long permanently marked transect was established within in each topographic position using a Laser Level (Leica Wild LNA 30™), with the coordinates for each transect permanently marked using a hand-held GPS device (Garmin™).

6.2.3. Abundance of Breeding Pintail and Other Waterfowl

Indicated Breeding Waterfowl Abundance (IBWA), an adapted version of the Indicator Breeding Bird (IBB) Abundance in use by the US Fish and Wildlife Service

(Dzubin 1969), was assessed for Pintail and Other Waterfowl at both Contra-Costa and Kitsim during the spring of 2003, 2004 and 2005. IBWA was assessed by censusing Pintail and all other species of waterfowl encountered on the study wetlands using a direct ground-based waterfowl count (Dzubin 1969). To maximize census intensity, three separate counts were made annually in early, mid and late May, and the largest of the three counts used in calculating annual IBWA of both Pintail and Other Waterfowl encountered on each replicate study wetland (IWWR Duck Survey Protocol *unpubl.*).

In addition to the census, waterfowl nests and broods incidentally encountered were documented for each experimental wetland at the Contra-Costa and Kitsim complexes. Nest locations were identified through searches at locations where any waterfowl species flushed into view. Identified nests were permanently marked with a global positioning system (GPS) to facilitate nest relocation during subsequent visits to determine nest fate, including hatched, abandoned, destroyed or unknown. Waterfowl brood sightings at each study site were recorded, along with any predators encountered during the waterfowl census periods in spring.

6.2.4. Habitat Structure and Density

Maximum community height (MCH) and visual obstruction reading (VOR) were measured within twenty, 0.25 m^2 sampling quadrats systematically placed along the permanent transect at each topographic position. However, MCH and VOR were not measured within flooded communities associated with the shallow and deep flooding zones at Contra-Costa where flooded conditions rendered such measurements impractical, nor in the deep marsh zones at Kitsim where the predominant vegetation was tall *T. latifolia*. MCH and VOR were measured within each quadrat using a 1.5 m graduated Robel pole, a meter-rule, and a 4 meter-rope in accordance with the technique developed by Robel et al. (1970) and modified for adaptation by Kirsch et al. (1978) and Higgins and Baker (1982).

6.2.5. Analyses

Indicated Breeding Waterfowl Abundance (IBWA) of each waterfowl species encountered, except Redhead, Lesser Scaup, Ring-necked Duck and Ruddy Duck, was calculated using the formula below:

$$\text{IBWA} = (2 \times \text{Pairs}) + (2 \times \text{Lone Males}) + (2 \times \text{Flocked Males} < 5) + (1 \times \text{Grouped Males \& Females} > 4).$$

The above equation was slightly modified to facilitate calculation of IBWA of Redhead, Lesser Scaup, Ring-necked Duck and Ruddy Duck as follows:

$$\text{IBWA} = (2 \times \text{Pairs}) + (1 \times \text{Lone Males}) + (1 \times \text{Flocked Males} < 5) + (1 \times \text{Lone Females}) + (1 \times \text{Grouped Males \& Females} > 4).$$

Subsequently, the IBWAs of all waterfowl species (excluding Pintail) were pooled together to determine the abundance of Other Waterfowl, and compared to that of Pintail.

By virtue of differences in the age of wetlands and types of flooding treatments implemented at Contra-Costa and Kitsum, the IBWAs and habitat structure data from each location were analyzed separately. Furthermore, wetlands at all locations were of variable sizes (Appendices III and IV). Given that wetland size positively influences the likelihood of wetland use by waterfowl (Stewart and Kantrud 1974), wetland area was used as a covariate in the statistical analysis of IBWA data.

Statistical analysis of IBWA data evaluated the effects of flooding treatment, census year, and flooding × census year interactions on the IBWAs of both Pintail and Other Waterfowl. Analysis used the GENMOD procedure of SAS (SAS Institute Inc. 2003) for analyzing count data (Pedan *unpubl.*). Statistical tests were considered significant at a chi square (χ^2) probability of 0.05 for all treatment and interaction effects.

Pre-flooding habitat structure and vegetation density at both Contra-Costa and Kitsim were used as covariates in performing the analyses of these data. Habitat structure and vegetation density datasets were initially tested for normality and found to be normally distributed based on a Shapiro-Wilk test ($P < 0.05$) (SAS Institute Inc. 2003). Statistical analyses used repeated measures ANCOVA for split-plot designs (Steele et al. 1997) to evaluate the effects of flooding treatment on successive annual measurements of MCH and VOR across topographic positions at Contra-Costa, while at Kitsim, an ANCOVA for split-plot designs was used to evaluate the effects of flooding treatment and cattle grazing on MCH and VOR across topographic positions, using Proc MIXED of SAS (SAS Institute Inc. 2003). Multiple LSmean comparisons on all significant treatment effects or interactions were performed using Tukey's test. Unless indicated otherwise, statistical tests were considered significant at $P \leq 0.05$ for all main treatment and interaction effects. Regression analysis was used to explore empirical relationships between IBWA and other variables such as wetland size, MCH and VOR.

Data on waterfowl nests and brood count, as well as predator abundance, were not analysed statistically because of their incidental nature. Instead, these data are presented as event summaries in Appendices XX to XXIII.

6.3. Results

6.3.1. IBWA of Pintail and Other Waterfowl at Contra-Costa

The IBWA of both Pintail and Other Waterfowl at Contra-Costa were affected by flooding treatment ($P < 0.0001$), census year ($P < 0.0001$), and a flooding × year interaction ($P < 0.0001$) (Table 6.1).

Initially, fall flooding in 2003 resulted in a greater IBWA of Pintail (17 per wetland) compared to the other treatments (Table 6.2A). However, significant reductions in Pintail occurred within fall flooded areas in 2004 and 2005. In contrast, spring flooding initially resulted in a low Pintail IBWA in 2003, but this number successively increased with subsequent spring flooding in each of 2004 and 2005, with IBWA values being greater than the fall treatment by the final year (Table 6.2A). Overall, both fall and spring flooded wetlands had similar average annual Pintail IBWA of 12 per wetland, substantially greater than that of natural wetlands, which had only 2 per wetland (Table 6.2A).

The IBWA of Other Waterfowl was greatest (83.0 ± 7.6) on fall flooded wetlands and lowest (7.3 ± 3.0) within naturally flooded wetlands (Table 6.2B). The flooding treatment × census year interaction indicated that fall flooded wetlands had the greatest IBWA of Other Waterfowl in both 2003 and 2005, with the least IBWA on natural wetlands in 2005 (Table 6.2B). The IBWAs of Other Waterfowl were similar between fall and spring flooded wetlands only during 2004 (Table 6.2).

Overall, the proportion of the IBWA of Pintail to that of Other Waterfowl across flooding treatments at Contra-Costa study area ranged from 14.2% on fall wetlands to a high of 23% on spring wetlands. Although natural wetlands had the least IBWA of both Pintail and Other Waterfowl, these wetlands had the largest proportion of Pintail (27%) in relation to that of Other Waterfowl.

6.3.2. IBWA of Pintail and Other Waterfowl at Kitsim

The IBWA of both Pintail and Other Waterfowl at Kitsim were affected by flooding treatment ($P < 0.05$) and census year ($P < 0.05$), but not the flooding × year interaction ($P > 0.20$) (Table 6.1). Among the flooding treatments investigated, overall Pintail IBWA values were greatest within (and similar among) the fall, spring and 1YNF wetlands, and lowest on the 2YNF wetlands (Table 6.3A). Notably, there was marked annual variation among the IBWA of Pintail at Kitsim, declining from 3.3 ± 1.2 in 2003 to 0.7 ± 0.1 in 2004 (Table 6.3A). However, post-treatment reflooding of 1YNF and 2YNF wetlands in 2005, coupled with distinct increases in Pintail abundance across all treatments, led to over 5-fold increase in the IBWA of Pintails in that year (Table 6.3A).

Similar to that of Pintail, the IBWAs of Other Waterfowl were similar among the fall, spring and 1YNF wetlands, all of which were greater than that of the 2YNF wetlands (Table 6.3B). Among census years, the IBWAs of Other Waterfowl in 2003 and 2004 were similar, but increased by nearly 70% following post treatment reflooding in 2005 (Table 6.3B).

Overall, the proportions of the IBWA of Pintail to that of Other Waterfowl across the Kitsim study area ranged from 8.6% in 2003 to 2.4% in 2004 (end of flooding treatment) with a subsequent rise to 9.1% following reflooding in 2005.

6.3.3. Relationship between IBWA and Wetland Size

At Contra-Costa, wetland size (covariate) significantly affected the IBWA of Pintail (*P* = 0.008) but not other waterfowl (*P* = 0.7) (Table 6.1). The IBWA of Pintail was noted to increase with wetland size in all three census years, but only for wetlands up to about 5 ha, after which Pintail IBWA values declined (Fig. 6.2). In contrast, the IBWA of Other Waterfowl demonstrated inconsistent annual relationships with wetland size (Fig. 6.2). In 2003, the IBWA of Other Waterfowl increased exponentially with wetland size. During the following two years, however, the IBWA of Other Waterfowl increased with moderate sized wetlands, but then declined with further increases in wetland size (beyond 5.5 ha in 2004, and beyond 8 ha in 2005) (Fig. 6.2).

At Kitsim, wetland size was a significant covariate affecting the IBWA of both Pintail (*P* = 0.05) and Other Waterfowl (*P* < 0.0001) (Table 6.1). At the onset of flooding treatment implementation in 2003, the IBWA of Pintail appeared to show a negative linear relationship with wetland size (Fig. 6.3). Notably, there was very minimal relationship of Pintail abundance to wetland size at the end of flooding treatments in 2004 (Fig. 6.3). However, the waterfowl census taken after reflooding in 2005 revealed a positive linear relationship with wetland size (Fig. 6.3).

Unlike that of Pintail, the IBWA of Other Waterfowl maintained a positive linear relationship with wetland size in all three census years (Fig. 6.3).

6.3.4. Waterfowl Habitat Structure and Density

6.3.4.1. Plant Community Height and Visual Obstruction at Contra-Costa

Flooding treatment alone did not affect either MCH or VOR at Contra-Costa ($P > 0.05$) (Table 6.4). However, VOR varied spatially across topographic positions and temporally across sampling years ($P < 0.0001$) (Table 6.4). Both MCH and VOR were affected by a flooding treatment × topographic position interaction ($P < 0.0001$), with VOR being further affected by the interactions of sampling year × flooding treatment ($P < 0.0001$), and sampling year × topographic position ($P < 0.0001$) (Table 6.4).

Fall and spring flooded wetlands at Contra-Costa generally had the greatest MCH values in the waterline zones while the lowest MCH occurred in both the upland and waterline zones of natural wetlands (Table 6.5). Significant differences occurred spatially in MCH values across spring flooded wetlands, being greatest in waterline zones and least on uplands (Table 6.5). No such differences occurred within the fall or naturally flooded wetlands (Table 6.5).

Fall flooded wetlands at Contra-Costa consistently maintained the greatest vegetation density (VOR) in all sampling years (Table 6.6A). Except for 2004 when spring flooded wetlands had a greater VOR, consistent with that of fall flooded wetlands, no differences existed between the VOR values of spring and naturally flooded wetlands in 2003 and 2005 (Table 6.6A). Notably, spring flooded wetlands experienced a 100% increase in VOR from 2003 to 2004, only to markedly decline again in 2005 (Table 6.6A). Naturally flooded wetlands did not experience any significant change in VOR across sampling years. Both uplands and waterline zones had similar VOR values in

2003 with significant spatial differences occurring in each of 2004 and 2005 (Table 6.6A). In 2004, waterline VOR values were nearly twice that of upland zones. This reversed in 2005, however, with uplands having significantly greater VOR values than the waterline zone (Table 6.6A).

Fall flooded wetlands at Contra-Costa generally had the greatest VOR values in the upland zones, followed by spring wetlands in the waterline zones (Table 6.6B). Overall, the least VOR occurred in the upland zones of natural wetlands (Table 6.6B).

6.3.4.2. Plant Community Height and Visual Obstruction at Kitsim

Flooding treatment affected both MCH and VOR at the end-of flooding treatment and post-reflooding sampling periods at Kitsim ($P \leq 0.06$) (Table 6.7). MCH (end – and post -) and VOR (end -) were affected by cattle grazing ($P < 0.05$), with an interaction of flooding × grazing evident for MCH and VOR at the end of applying the flooding treatments in 2004 ($P \leq 0.06$) (Table 6.7).

Both MCH and VOR also varied spatially across topographic positions ($P < 0.0001$) at both sampling times, with significant position × grazing interactions during the end of flooding treatment period ($P < 0.05$). While MCH was affected by a position × flooding treatment interaction during both sampling periods ($P < 0.05$), VOR was unaffected by this interaction ($P > 0.1$) (Table 6.7).

After cessation of the flooding treatments in 2004, MCH was similar and greatest on both the fall and spring flooded wetlands, but least on the 1YNF and 2YNF wetlands (Tables 6.8). Comparison of grazed and ungrazed sites indicated MCH to be significantly greater at the latter, although this difference occurred primarily on fall flooded wetlands, with minor to no differences within the other flooding treatments between grazed and ungrazed areas (Table 6.8).

Spatial differences in MCH also occurred at the end of the flooding treatments at Kitsim, where the greatest MCH values were associated with the wet meadow zone, followed by the dry meadow zone, and then uplands (Table 6.8). The position × grazing interaction indicated that grazing reduced MCH to the greatest extent within the wet and dry meadows rather than on uplands (Table 6.8).

Responses within the VOR data immediately after the flooding treatments ended were partly similar to those of MCH. For example, similar to MCH, VOR values were greatest for wet meadows, followed by dry meadows and then uplands, with grazing leading to a decline in VOR, particularly within the wet meadows (Table 6.8). While overall VOR values were greatest in the spring flooded treatment, the fall treatment tended to be low in VOR, similar to that of the 1YNF (Table 6.8). This response appeared to be at least partly due to the strong influence of grazing within this flooding treatment, as grazing had the greatest influence in decreasing VOR within fall flooded areas compared to all the other treatments (Table 6.8).

The interaction of flooding treatment × topographic position on MCH at both the end of the flooding treatments and post reflooding indicated that vegetation responses were spatially variable across positions, as well as among flooding treatments at both sampling times. For example, during the end of treatment sampling, MCH values were similar among all flooding treatments within both uplands and dry meadows. However, significant differences occurred among flooding treatments at the wet meadow position (Table 6.9). In particular, the greatest MCH values at this landscape position were found in the fall and spring flooded wetlands, followed by the 2YNF and 1YNF treatments (Table 6.9). Similar trends were evident one year later following reflooding with no differences among treatments within the upland position. Unlike the year before, dry meadows had greater MCH within the spring and 1YNF treatments. Wet meadows continued to have the greatest MCH, but only under a fall, spring or 1YNF flood treatment (Table. 6.9).

Assessment of vegetation responses at Kitsim after reflooding in 2005 indicated that greater MCH and VOR values were associated with both spring and 1YNF wetlands, with the lowest occurring on the fall and 2YNF wetlands (Table 6.10). While MCH was greater within ungrazed sites during post-reflooding sampling, VOR values remained similar between the two (Table 6.10). Strong differences remained evident in the MCH and VOR values among positions after reflooding (Table 6.10), similar to those apparent the year before (i.e., wet meadow>dry meadow>uplands).

6.3.5. Relationship between IBWA and Maximum Community Height (MCH)

The IBWA of Pintail at Contra-Costa displayed little relationship to upland MCH in 2003 or 2005 (Fig. 6.4). The IBWA of Other Waterfowl, however, indicated a positive linear relationship ($P < 0.05$) with upland MCH in both years (Fig. 6.4).

Compared to the uplands, there were significant associations between the IBWA of both Pintail and Other Waterfowl, and observed MCH in the waterline zones, but only in 2005. There was a positive linear response for both waterfowl groups to increases in MCH in that year (Fig. 6.5).

At Kitsim, both the end of flooding and post reflooding assessments indicated no relationship between the IBWA of Pintail, nor Other Waterfowl, and the MCH on either upland (Fig. 6.6) or dry meadow (Fig. 6.7) zones (with the exception of a very weak relationship in the dry meadow zones at the end of flooding treatment – Fig. 6.7).

6.3.4. Relationship between IBWA and Visual Obstruction Reading (VOR)

Similar to MCH results in 2003, poor relationships occurred between upland VOR values and the IBWA of Pintail and Other Waterfowl (Fig. 6.8). In 2005, only the IBWA of Other Waterfowl had a relationship with upland VOR, as demonstrated through a strong positive linear relationship between the IBWA of Other Waterfowl and upland VOR (Fig. 6.8). Overall, relationships between the IBWA of Pintail or Other Waterfowl and waterline VOR values were again weak, with only the IBWA of Other Waterfowl maintaining a strong positive linear relationship with waterline VOR in 2005 (Fig. 6.9).

The relationship of Pintail and Other Waterfowl abundance to upland (Fig. 6.10) and dry meadow (Fig. 6.11) VOR values during end of flooding treatment and post reflooding sampling at Kitsim paralleled those of MCH (Figs. 6.6 and 6.7). The IBWA of both Pintail and Other Waterfowl showed minimal association with VOR in the upland and dry meadow zones at either the end of flooding treatment or reflooding periods.

Overall, the relationships of the IBWAs of Pintail and Other Waterfowl to the habitat structure variables assessed, particularly at Contra-Costa, indicated that the IBWAs had stronger relationships with VOR measurements than those of MCH, as indicated by the higher regression coefficient (R^2) values (Figs. 6.4 – 6.11).

6.4. Discussion

6.4.1. Pintail and Other Waterfowl Abundance

Wetland availability and abundance in spring have been identified as critical factors affecting the recruitment of waterfowl in the Prairies (Stewart and Kantrud 1973, Stewart and Kantrud 1974, Austin and Miller 1995, Koeln et al. 1996). In particular, the presence of many seasonal and semipermanent wetlands interspersed with short emergent vegetation on the prairie landscape attracts Pintails to breed and nest (Stewart and Kantrud 1974, Kaminski and Prince 1984). Results of the present study supported this observation and indicated that wetland availability in spring is a critical determinant of the abundance of breeding waterfowl on the prairie landscape, particularly Pintails. Overall, compared to natural flooding from snow melt and precipitation, anthropogenic flooding in either fall or spring increased Pintail abundance on newly created wetlands at Contra-Costa. Spring flooding led to a greater increase in Pintail abundance at Contra-Costa compared to fall flooding. Overall, Pintail abundance at Contra-Costa represented only 14.2% of Other Waterfowl on new fall wetlands, and 23% on new spring wetlands.

The largest difference in Pintail abundance between fall and spring wetlands at Contra-Costa occurred in 2003 and 2005. Pintail were more abundant in fall wetlands during 2003 while spring wetlands were apparently preferred in 2005. Abundant Pintail numbers on fall wetlands in 2003 may be due to food availability (Bataille and Baldassarre 1993). As fall wetlands had already been flooded the previous year, it is likely that invertebrate production within these wetlands was initially more abundant compared to wetlands first flooded in the spring of 2003.. Thus, Pintails appeared to initially prefer fall wetlands as water availability influences food availability (Braithwaite and Frith 1969), which in turn, remains a critical indicator of habitat quality for reproductive purposes (Braithwaite and Frith 1969, Krapu and Reinecke. 1992, Bataille and Baldassarre 1993). After 3 consecutive years of flooding, however, water levels in May during the breeding survey may have been greater and more stable in spring flooded wetlands, causing Pintails to prefer them instead.

Initial fall flooding in 2003 might have affected biological activities less in the newly created wetlands at Contra-Costa, while subsequent annual fall flooding likely led to the maintenance of extended anaerobic conditions detrimental to certain riparian and aquatic plants (Mitsch and Gosselink 2000). Riparian and aquatic plants are needed to provide habitats for aquatic invertebrates used as food by many species of waterfowl, particularly Pintails (Murkin and Kadlec 1986a, Foote and Hornung 2005). The preceding factors might have also led to the loss of suitable habitats needed as escape cover for waterfowl broods. Thus, it may be reasonable to theorize that by avoiding extended flooding throughout winter (7 to 8 months), spring flooding may have prevented the maintenance of anoxic conditions detrimental to certain plants.

In 2004, fall and spring wetlands at Contra-Costa had similar Pintail abundance, which may be due to the fact that each flooding treatment had experienced recent flooding and were therefore similar in tall vegetation structure, and most importantly, visual obstruction at the waterline zone. Previous studies indicate Pintail pairs are attracted to shallow and semi-permanent wetlands with emergent vegetation and low grassland cover on adjacent uplands (Stewart and Kantrud 1973, Kaminski and Weller 1992). It is important to note from the results of the present study that vegetation density (visual obstruction) was moderate to high in the waterline zones (synonymous with riparian zones) of fall and spring flooded wetlands in 2004. This coincided with similarly high Pintail abundance between the two flooding treatments, suggesting that riparian vegetation density may also be critical in attracting Pintails to utilize Dry Mixed Grass Prairie wetlands. Abundant vegetation in the waterline zone has the benefit of providing source of forage and escape corridors for many open grassland wildlife species including Pintail broods.

Unlike Pintails, Other Waterfowl at Contra-Costa consistently favored fall flooded wetlands over those flooded in spring. Results of the present study suggest that annual fall flooding may benefit Other Waterfowl more than Pintails. Fall flooded wetlands had taller vegetation structure, including height and visual obstruction, especially in sub-irrigated upland and waterline zones. It is important to note that Other Waterfowl comprised of all other waterfowl species except Pintail (Appendix XIX), and these species altogether have a broader range of habitat preferences, ranging from small to large wetland size, and shallow to deep water body, and short to tall vegetation structure. The abundance of Other Waterfowl was similar between fall and spring flooding treatments at Contra-Costa in 2004, likely due to the similar vegetation structure around wetlands that received fall and spring flooding treatments, as previously discussed. Overall, these results at Contra-Costa emphasize the uniqueness of Pintail habitat requirements in relation to Other Waterfowl in the Dry Mixed Grass Prairie (Koeln et al. 1996).

At Kitsim, both Pintail and Other Waterfowl abundance were lowest on wetlands dried for 2 years (2YNF), likely because of a lack of moisture directly associated with the cessation of flooding. This result was expected, as loss of free standing water in wetlands renders them less suitable for use by breeding waterfowl (Koeln et al. 1996), and wetland moisture availability remains the key factor regulating waterfowl use of wetlands (Stewart and Kantrud 1974). Nevertheless, both Pintail and Other Waterfowl still utilized the flood cessation wetlands at Kitsim, although Pintail appeared to be adversely impacted by flood cessation. Notably, flood cessation wetlands were at least 25% flooded (by area) during the spring of each census year (Appendix IV) as a result of moisture recharge during snowmelt.

There was also strong temporal variation in the IBWA of Pintail at Kitsim, declining from 2003 to 2004, with a subsequent increase in 2005. Wetland moisture fluctuation has been reported to affect breeding waterfowl abundance (Stewart and Kantrud 1974) and food availability (Braithwaite and Frith 1969, Frederickson and Heitmeyer 1991) in the prairies. While the flood cessation treatments examined here led to a temporary reduction in Pintail use of these wetlands, subsequent reflooding in 2005 increased Pintail abundance, likely due to the prompt return of wetland conditions and associated habitat quality (i.e., food availability).

The proportional representation of Pintail abundance to Other Waterfowl across the Kitsim study area was much lower than at Contra-Costa, ranging from 8.6% in 2003 to 2.4% in 2004 (end of flooding treatment), with a subsequent rise to 9.1% following reflooding in 2005. This observation highlights the fact that flood cessation heavily impacted waterfowl abundance, and Pintail in particular, during times of low water availability. It is important to note that the proportional representation of Pintails to Other Waterfowl on previously dried Kitsim wetlands could not parallel that of newly created wetlands at Contra-Costa. This indicates that older wetlands at Kitsim, presumably due to their excessive vegetative cover in the form of *T. latifolia* (Chapter 4), provided less than optimum habitat for Pintails compared to the more open wetlands at Contra-Costa.

Wetland size in general appeared to influence the abundance of Pintail, similar to other studies (Stewart and Kantrud 1974). Results of the present study suggest Pintails have greater affinity for small wetlands (less than 5 ha) in the prairies. This is likely because smaller wetlands are shallow and range from ephemeral to semipermanent, and are more likely to be interspersed with the short structured vegetation preferred by Pintails (Kaminski and Prince 1984, Kaminski and Weller 1992). In contrast, Other Watefowl had greater tolerance for larger wetlands up to about 8 ha at Contra-Costa, and at Kitsim, appeared to have no upper limit in preferred wetland size, likely because of their wide range of habitat requirements and foraging opportunities.

6.4.2. Habitat Structure

Wetland moisture availability affected the structure (MCH) and density (VOR) of vegetation associated with all study wetlands at Contra-Costa and Kitsim. Spatial variation typically reflected lower values on uplands to the greatest in low lying topographic zones of various flooding treatments. Thus, soil moisture gradients across the landscape appear critical in dictating the structure and density of vegetation along wetlands used by breeding waterfowl in the Dry Mixed Grass Prairie.

An interesting result from Contra-Costa indicates that while fall flooding produced greater VOR in upland zones, spring flooding led to a greater VOR in the waterline zones, with the lowest VOR in uplands of natural wetlands. Fall flooding extending over the winter months likely led to the maintenance of anaerobic conditions detrimental to some of the plant propagules initially found in the lower topographic zones, but concurrently led to a rise in water table to the benefit of sub-irrigated upland vegetation, which takes up moisture from phreatic depths. On the other hand, spring wetlands appeared to depend heavily on the short-term moisture available from spring flooding, which could therefore support the growth of vegetation commonly found in these riparian and shallow flooding zones, in turn resulting in increased VOR at the waterline position.

At Kitsim, the greatest MCH and VOR values were associated with the wet meadow zone while the lowest occurred on uplands. Both the 1YNF and 2YNF treatment decreased in MCH and VOR at the dry and wet meadow positions at the end of flooding treatment in 2004. Moreover, the 2YNF remained lower in MCH and VOR in the dry and wet meadow zones with reflooding compared to the other treatments. Notably, the dynamics of both Pintail and Other Waterfowl abundance in response to the flooding treatments paralleled those of MCH and VOR, highlighting the importance of riparian vegetation structure (in addition to moisture availability) in affecting waterfowl abundance in the Dry Mixed Grass Prairie.

At the end of the flooding treatments at Kitsim, significant differences occurred in MCH among flooding treatments at the wet meadow zone, with the greatest values occuring on fall and spring wetlands, and the lowest on 1YNF and 2YNF wetlands. Following reflooding, wet meadows continued to have the greatest MCH, but only on fall, spring and 1YNF wetlands. This observation indicates that reflooding led to vegetation height response on all but 2YNF wetlands, suggesting that there was greater residual effect of vegetation decline with two years of flood cessation. This result has important implications for the objective of managing established Kitsim wetland habitats to achieve the low-structured vegetation preferred by Pintail.

Areas exposed to cattle grazing at Kitsim had lower MCH and VOR compared to ungrazed areas, particularly in dry and wet meadows. Grazing is an important disturbance regime known to significantly impact herbage availability (Willms 1988, Asamoah et al. 2003) and vegetation structure (Foote and Hornung 2005, Koper and Schmiegelow 2006a) in riparian zones. The reduction in MCH and VOR in grazed wet and dry meadow zones in the present study suggests that herbage removal through cattle grazing affected both the structure and density of vegetation at these locations. Thus, a combination of flood cessation and cattle grazing may have the benefit of reducing tall and dense vegetation, which otherwise may remain unsuitable as habitat for Pintail and many other species of waterfowl. Beneficial grazing impacts, coupled with reduced vegetation stature, particularly in the 2YNF treatment, may account for the prompt recovery of Pintail IBWA at Kitsim in 2005 to levels above that of 2003 prior to the implementation of flooding treatments. Moreover, Other Waterfowl also increased in 2005 to the greatest levels observed, reflecting more than just beneficial impacts on Pintail. Notwithstanding the beneficial grazing impacts, the potential of nutrient enrichment in wetlands as a result of cattle grazing cannot escape being mentioned.

Among the vegetation structure and density measurements assessed, the present study found MCH to be consistently correlated to changes in IBWA, although MCH was overall a relatively poor predictor of waterfowl abundance. Instead, IBWA was found to be more strongly correlated with VOR, as indicated by higher regression coefficient (R^2)

values, suggesting that where comprehensive VOR data are available, they may be a better predictor of Pintail and Other Waterfowl abundance.

6.5. Conclusions and Management Implications

Anthropogenic flooding appears to be an effective means of enhancing habitat for waterfowl in the Dry Mixed Grass Prairie. While fall flooding initially caused a sharp increase in the abundance of Pintail and Other Waterfowl, spring flooding led to greater Pintail abundance by the third year of flooding. In contrast, Other Waterfowl were consistently more abundant on fall flooded wetlands. Low numbers of Pintail and Other Waterfowl on naturally flooded wetlands at Contra-Costa suggests that anthropogenic flood augmentation is critical to increasing the abundance of breeding Pintails and Other Waterfowl in the Dry Mixed Grass Prairie. In addition to moisture availability, results of this study indicated that wetland size and vegetation density are important predictors of wetland use by Pintail and Other Waterfowl. In particular, Pintails are attracted to smaller, relatively shallow wetlands with moderately dense riparian vegetation.

Results from Kitsim suggest that while two or more years of flood cessation may be detrimental to the IBWA of both Pintails and Other Waterfowl, subsequent reflooding resulted in increased Pintail and Other Waterfowl abundance. Thus, improvements in waterfowl abundance may justify the short-term habitat modification under flood cessation intended to control *T. latifolia* (Chapter 4) despite the initial adverse effects on prairie breeding waterfowl, especially Pintail. Whether longer-term improvements in waterfowl numbers occur, including those associated with even longer drying periods, remains unclear and require further testing.

Table 6.1: Summary of 'Wald' statistics for type 3 chi-square analysis of the effects of flooding treatment, census year and their interaction, on the IBWA values of Northern Pintail and Other Waterfowl at Contra-Costa and Kitsim during May 2003, 2004 and 2005.

Source	df	Northern Pintail		Other Waterfowl	
		χ^2	Pr > χ^2	χ^2	Pr > χ^2
Contra-Costa					
Wetland Size (*Covariate*)	1	6.95	**0.008**	0.17	0.7
Flooding Treatment	2	439.5	**<0.0001**	1487.9	**<0.0001**
Census Year	2	856.8	**<0.0001**	2155.5	**<0.0001**
Flooding x Year	3	1118.9	**<0.0001**	3263.5	**<0.0001**
Kitsim					
Wetland Size (*Covariate*)	1	3.82	**0.05**	15.73	**<0.0001**
Flooding Treatment	3	10.27	**0.02**	30.34	**<0.0001**
Census Year	2	19.98	**<0.0001**	6.83	**0.03**
Flooding x Year	6	7.91	0.24	4.27	0.64

Table 6.2: Variation in the IBWA of (A) Northern Pintail and (B) Other Waterfowl in response to fall, spring and natural flooding treatments during Indicated Breeding Waterfowl surveys at Contra-Costa from spring 2003 to 2005. Flooding treatment × census year interaction means with different lowercase letters differ ($P < 0.05$). Flooding treatment grand means with different uppercase letters differ ($P < 0.05$).

(A) Northern Pintail

Flooding Treatment	Census Year 2003	 2004	 2005	***Mean (Flooding)***	*(S.E.)*
	-------------------Pintail IBWA--------------------				
Fall Flooding	16.5 a	10.0 b	9.0 b	***11.8 A***	***(1.9)***
Spring Flooding	5.5 c	12.0 b	19.0 a	***12.2 A***	***(2.2)***
Natural Flooding	4.0 c	2.0 c	0.0 d	***2.0 B***	***(0.9)***

(B) Other Waterfowl

Flooding Treatment	Census Year 2003	 2004	 2005	***Mean (Flooding)***	*(S.E.)*
	---------------Other Waterfowl IBWA--------------				
Fall Flooding	87.8 a	65.0 b	96.3 a	***83.0 A***	***(7.6)***
Spring Flooding	26.0 c	72.0 b	61.0 b	***53.0 B***	***(8.3)***
Natural Flooding	10.0 d	12.0 d	0.0 e	***7.3 C***	***(3.0)***

Table 6.3: Variation in the IBWA of (A) Northern Pintail and (B) Other Waterfowl in response to fall and spring flooding, as well as two flood cessation treatments (1YNF and 2YNF) during Indicated Breeding Waterfowl surveys at Kitsim from spring 2003 to 2005. Census year grand means with different uppercase letters differ ($P < 0.05$). Flooding treatment grand means with different uppercase letters differ ($P < 0.05$).

(A) Northern Pintail

Flooding Treatment	Census Year			***Mean (Flooding)***	***(S.E.)***
	2003	2004	2005		
	-------------------*Pintail IBWA*------------------------				
Fall Flooding	1.5	0.5	8.3	***3.4 A***	***(2.0)***
Spring Flooding	3.5	1.0	6.5	***3.7 A***	***(1.3)***
1YNF	7.3	0.8	4.5	***4.2 A***	***(1.5)***
2YNF	1.0	0.5	1.5	***1.0 B***	***(0.2)***
Mean (Year)	***3.3 B***	***0.7 C***	***5.2 A***		
(S.E)	***(1.2)***	***(0.1)***	***(1.3)***		

(B) Other Waterfowl

Flooding Treatment	Census Year			***Mean (Flooding)***	***(S.E.)***
	2003	2004	2005		
	----------------*Other Waterfowl IBWA*--------------				
Fall Flooding	52.8	36.0	55.0	***47.9 A***	***(4.9)***
Spring Flooding	43.0	40.5	81.8	***55.1 A***	***(10.9)***
1YNF	45.5	29.5	48.0	***41.0 A***	***(4.7)***
2YNF	12.0	10.5	44.0	***22.2 B***	***(8.9)***
Mean (Year)	***38.3 B***	***29.1 B***	***57.2 A***		
(S.E)	***(7.8)***	***(5.7)***	***(7.4)***		

Table 6.4: Summary of statistical tests indicating *P-values* of the effects of flooding treatment, depth of flooding (topographic position), and sampling year on MCH (maximum plant community height) and VOR (visual obstruction readings) at Contra-Costa.

Effect	df	Maximum Community Height	Visual Obstruction Reading
		----------*P* Value---------	
Pre-flooding (Covariate)	*1*	0.89	0.93
Flooding Treatment	2	0.37	0.15
Topographic Position	1	0.16	**<0.0001**
Flooding x Position	2	**0.0001**	**<0.0001**
Sampling Year	2	0.62	**<0.0001**
Year x Flooding	4	0.16	**<0.0001**
Year x Position	2	0.95	**<0.0001**
Year x Flooding x Position	4	0.18	0.09

Table 6.5: Variation in July MCH (maximum plant community height - dm) in response to fall, spring and natural flooding treatments at Contra-Costa. Flooding × position means with different lowercase letters differ ($P < 0.05$).

Flooding Treatment	Topographic Position		***Mean***	***(SE)***
	Upland	Waterline		
Fall Flooding	6.9 a	5.6 ab	***6.3***	***(0.7)***
Spring Flooding	4.2 b	7.5 a	***5.9***	***(1.7)***
Natural Flooding	4.9 b	4.8 b	***4.8***	***(0.1)***

Table 6.6: Annual variation in July VOR (visual obstruction readings - dm) in response to (A) flooding treatments, topographic positions, and (B) their interactions across landscapes at Contra-Costa. Within a factor (A), treatment level × sampling year means with different lower case letters differ ($P < 0.0001$); grand means of sampling years with different uppercase letters differ ($P < 0.0001$). Flooding treatment × topographic position means (B) with different lowercase letters differ ($P < 0.0001$); grand means of topographic position with different uppercase letters differ ($P < 0.0001$).

(A)

Factor	Level	Sampling Year		
		2003	2004	2005
Flooding Treatment	Fall	2.7 a	2.4 ab	2.0 b
	Spring	1.1 c	2.2 b	0.9 c
	Natural	1.1 c	1.4 c	1.0 c
	Mean	***1.6 AB***	***2.0 A***	***1.3 B***
	(SE)		***(0.2)***	
Topographic Position	Upland	1.6 bc	1.4 c	2.0 b
	Waterline	1.7 bc	2.6 a	0.5 d

(B)

Flooding Treatment	Topographic Position	
	Upland	Waterline
Fall	3.2 a	1.6 c
Spring	0.8 f	2.0 b
Natural	1.1 e	1.3 d
Mean	***1.7 A***	***1.6 B***
(SE)	***(0.02)***	

Table 6.7: Summary of statistical tests indicating *P*-values of the effects of four flooding treatments and cattle grazing on July MCH (maximum plant community height) and VOR (visual obstruction readings), across three topographic positions during end of flooding treatment and post reflooding at Kitsim.

Effect	df	End of Treatment		Post Reflooding Treatment	
		MCH	VOR	MCH	VOR
		-P Value-			
Pre-flooding (Covariate)	*1*	***<0.0001***	*0.08*	***0.007***	*0.21*
Flooding	3	0.06*	**0.05**	**0.005**	**0.02**
Cattle Grazing	1	**0.01**	**0.04**	**0.01**	0.10
Flooding x Grazing	3	0.06*	0.06*	0.12	0.42
Topographic Position	2	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Position x Flooding	6	**0.002**	0.71	**0.02**	0.47
Position x Grazing	2	**0.002**	**0.02**	0.32	0.67
Position x Flooding x Grazing	6	0.83	0.14	0.67	0.96

* $P = 0.06$ considered to be biologically significant.

Table 6.8: Landscape variation in maximum plant community height - MCH (dm) and visual obstruction reading - VOR (dm) in response to four flooding treatments under ungrazed and grazed conditions during end-of-flooding treatment sampling at Kitsim in July of 2004. Within a response variable, interaction means with different lowercase letters differ ($P < 0.05$). Within a response variable, grand means of cattle grazing, flooding treatment or topographic position with different uppercase letters differ ($P < 0.05$).

Factor	Level	MCH			VOR		
		Ungrazed	Grazed	**Mean**	Ungrazed	Grazed	**Mean**
Flooding	Fall	7.7 a	5.2 d	**6.4 A**	2.1 a	0.7 d	**1.4 B**
	Spring	6.8 b	6.9 b	**6.8 A**	2.2 a	1.9 a	**2.1 A**
	1YNF	6.0 c	5.3 d	**5.6 B**	1.4 bc	1.0 cd	**1.2 B**
	2YNF	6.1 c	5.5 cd	**5.8 B**	1.6 ab	1.8 a	**1.7 AB**
	Mean	***6.6 A***	***5.7 B***		***1.8 A***	***1.4 B***	
	(SE)	***(0.2)***			***(0.14)***		
Position	Upland	4.1 d	4.7 cd	**4.4 C**	0.7 c	0.9 c	**0.8 C**
	Dry Meadow	6.5 b	5.5 c	**6.0 B**	1.8 b	1.5 b	**1.7 B**
	Wet Meadow	9.4 a	6.9 b	**8.1 A**	3.0 a	1.6 b	**2.3 A**
	(SE)	***(0.3)***			***(0.28)***		

Table 6.9: Landscape variation in maximum plant community height – MCH (dm) in response to four flooding treatments during end of treatment and post-reflooding sampling at Kitsim in July 2004 and 2005, respectively. Within a response variable, flooding × position means with different lowercase letters differ ($P < 0.5$).

Flooding Treatment	End of treatment MCH			Post reflooding MCH		
	Upland	Dry Meadow	Wet Meadow	Upland	Dry Meadow	Wet Meadow
Fall	3.9 e	5.5 cd	10.0 a	3.6 f	6.1 de	10.4 a
Spring	4.6 de	6.6 bc	9.3 a	4.5 ef	9.5 ab	10.4 a
1YNF	5.0 de	6.0 c	5.9 c	4.7 ef	8.3 bc	9.0 ab
2YNF	4.1 de	5.9 c	7.3 b	4.6 ef	6.1 de	7.2 cd
(SE)		***(0.5)***			***(0.7)***	

Table 6.10: Landscape variation in maximum plant community height – MCH (dm) and visual obstruction reading – VOR (dm) in response to four flooding treatments under ungrazed and grazed conditions during post-reflooding sampling at Kitsim in July 2005. Within a treatment factor and response variable, means of treatment levels with different lowercase letters differ ($P < 0.05$).

Factor	Level	MCH	VOR
Flooding Treatment	Fall	6.7 bc	2.5 b
	Spring	8.1 a	3.2 a
	1YNF	7.3 ab	3.3 a
	2YNF	5.9 c	2.4 b
	(SE)	***(0.4)***	***(0.3)***
Cattle Grazing	Ungrazed	7.6 a	3.1
	Grazed	6.5 b	2.6
	(SE)	***(0.3)***	***(0.2)***
Topographic Position	Upland	4.4 c	1.3 c
	Dry Meadow	7.5 b	2.8 b
	Wet Meadow	9.3 a	4.4 a
	(SE)	***(0.4)***	***(0.2)***

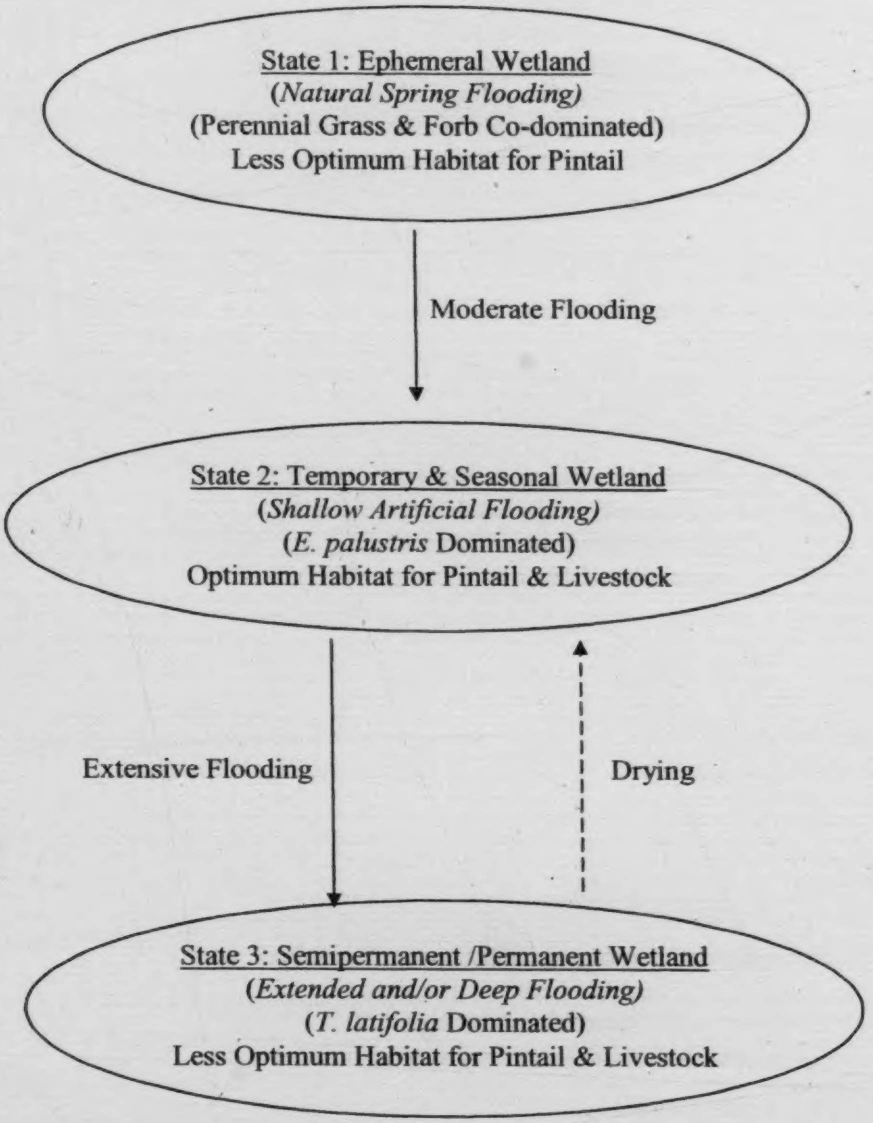

State 1: Ephemeral Wetland
(Natural Spring Flooding)
(Perennial Grass & Forb Co-dominated)
Less Optimum Habitat for Pintail
Moderate Flooding
State 2: Temporary & Seasonal Wetland
(Shallow Artificial Flooding)
(E. palustris Dominated)
Optimum Habitat for Pintail & Livestock
Extensive Flooding
Drying
State 3: Semipermanent /Permanent Wetland
(Extended and/or Deep Flooding)
(T. latifolia Dominated)
Less Optimum Habitat for Pintail & Livestock

Fig. 6.1: Theorized model of vegetation succession following wetland creation in the Dry Mixed Grass Prairie of southeastern Alberta, Canada. State 2 constitutes the desired plant community (DPC) that provides the habitat mosaic optimum for Northern Pintail and rangeland cattle. While moderate and extensive flooding of newly created wetlands may facilitate succession to states 2 and 3, respectively, wetland drying may facilitate community change from state 3 to 2 (the DPC).

✓

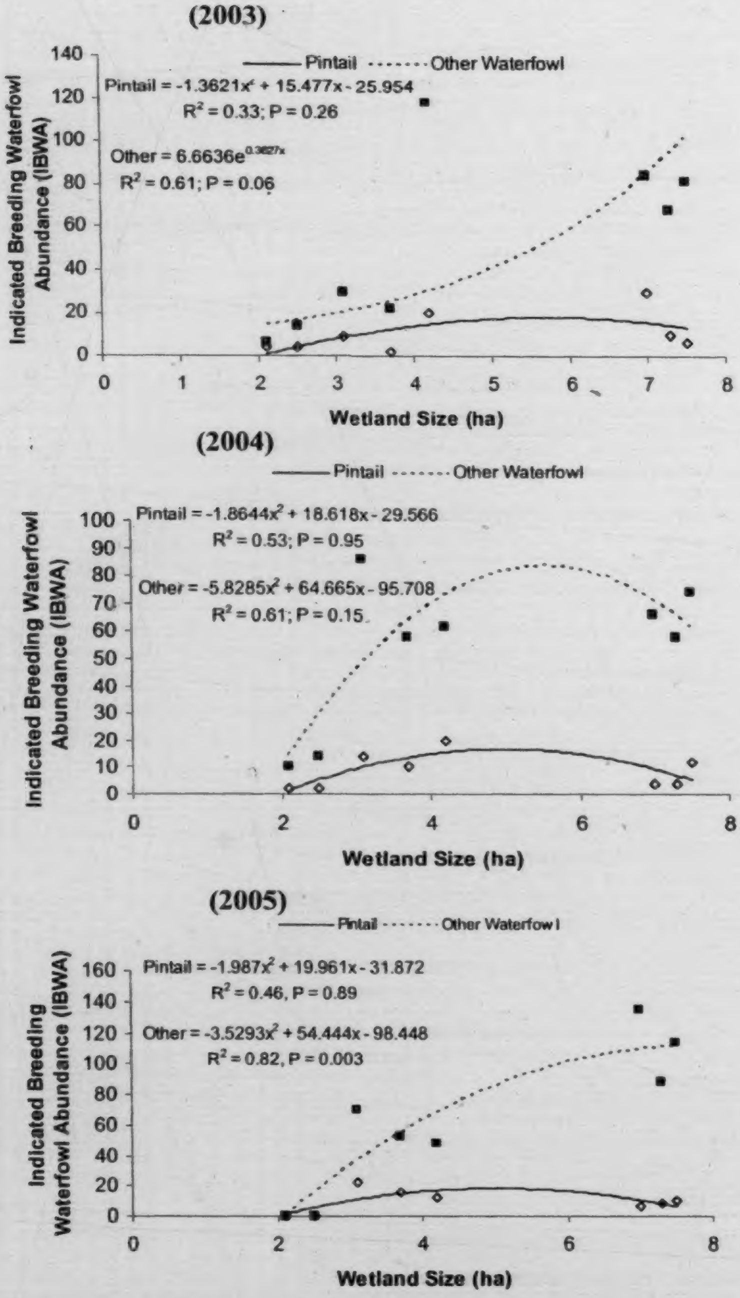


Fig. 6.2: Relationship between wetland size and IBWA of Pintail and Other Waterfowl during each of three census years at Contra-Costa.

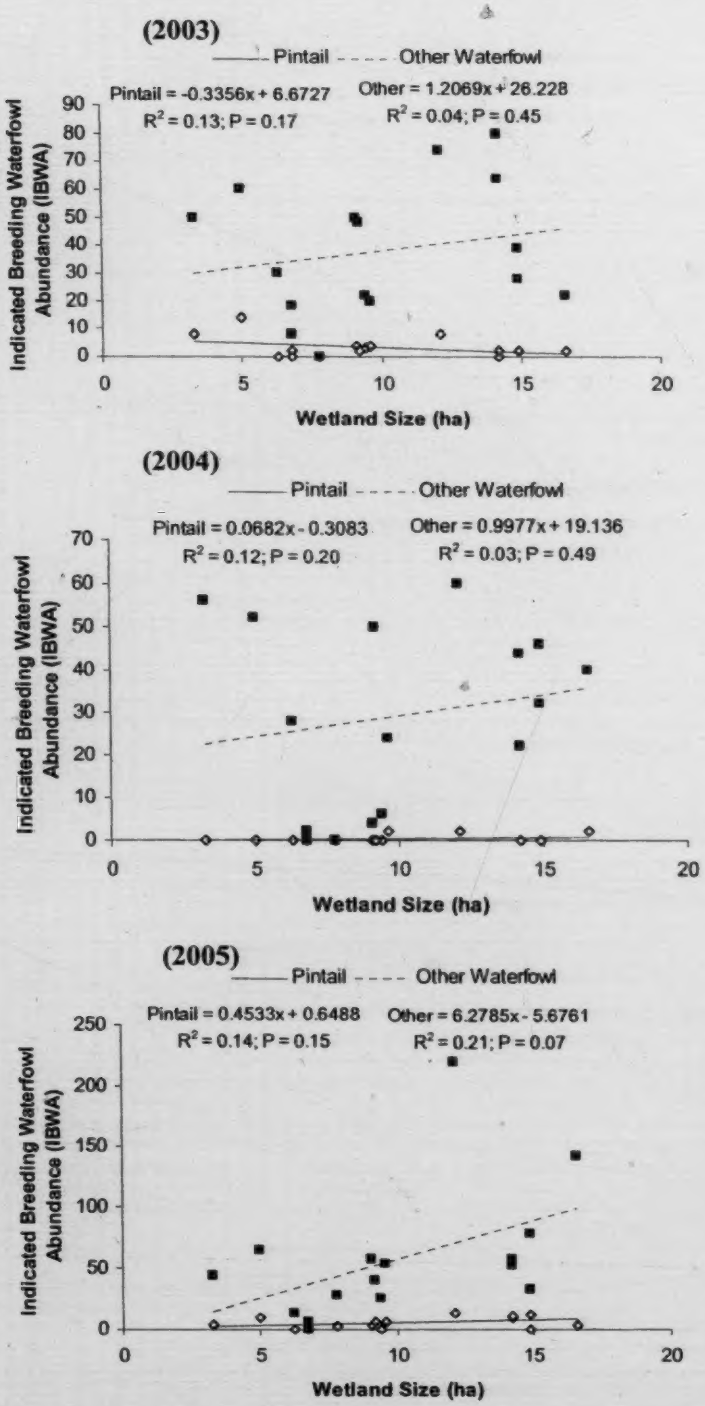
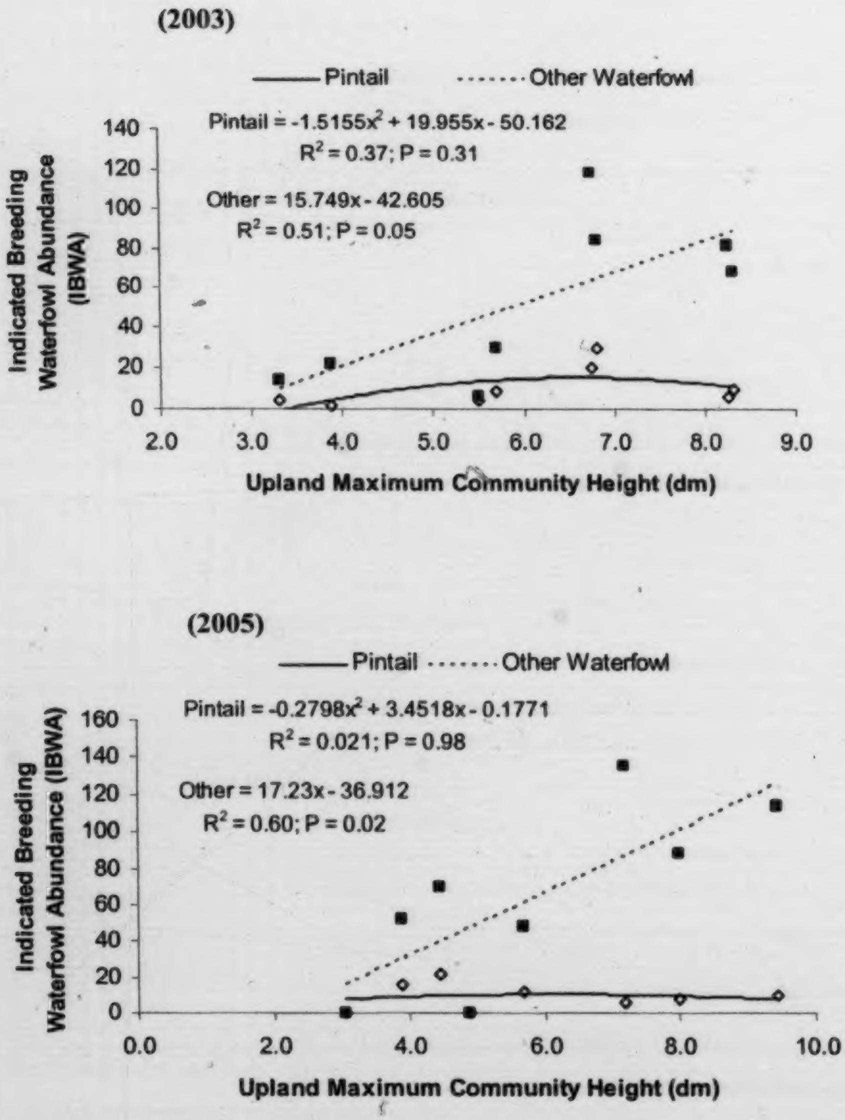
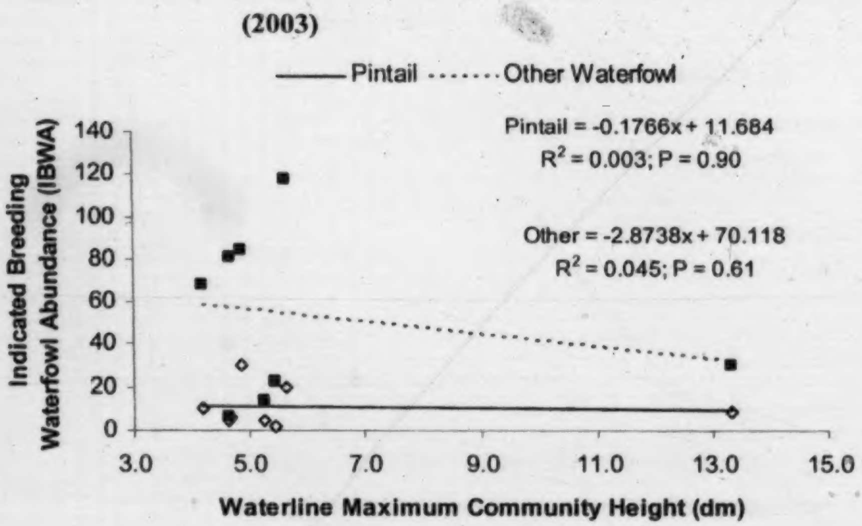


Fig. 6.3: Relationship between wetland size and IBWA of Pintail and Other Waterfowl during each of three census years at Kitsim.


(2003)

(2005)

Fig. 6.4: Relationships of IBWA of Pintail and Other Waterfowl to Upland Maximum Community Height at Contra-Costa in 2003 and 2005.



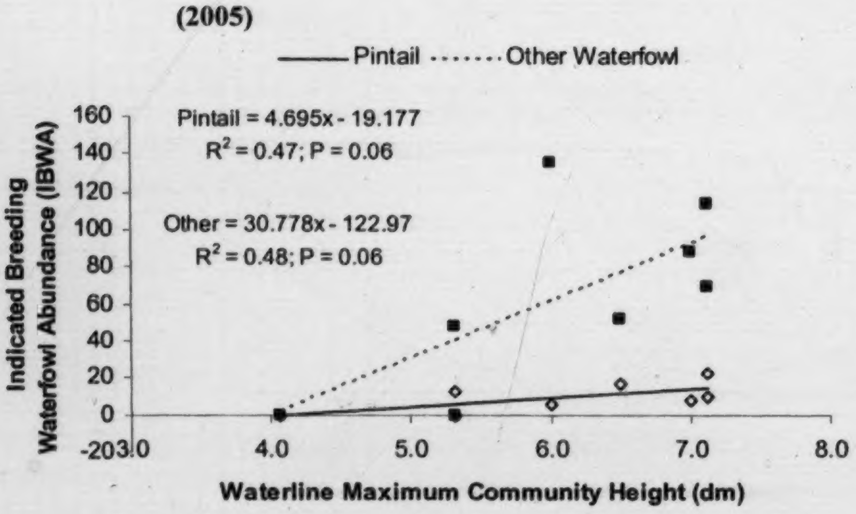


Fig. 6.5: Relationships of IBWA of Pintail and Other Waterfowl to Waterline Maximum Community Height at Contra-Costa in 2003 and 2005.

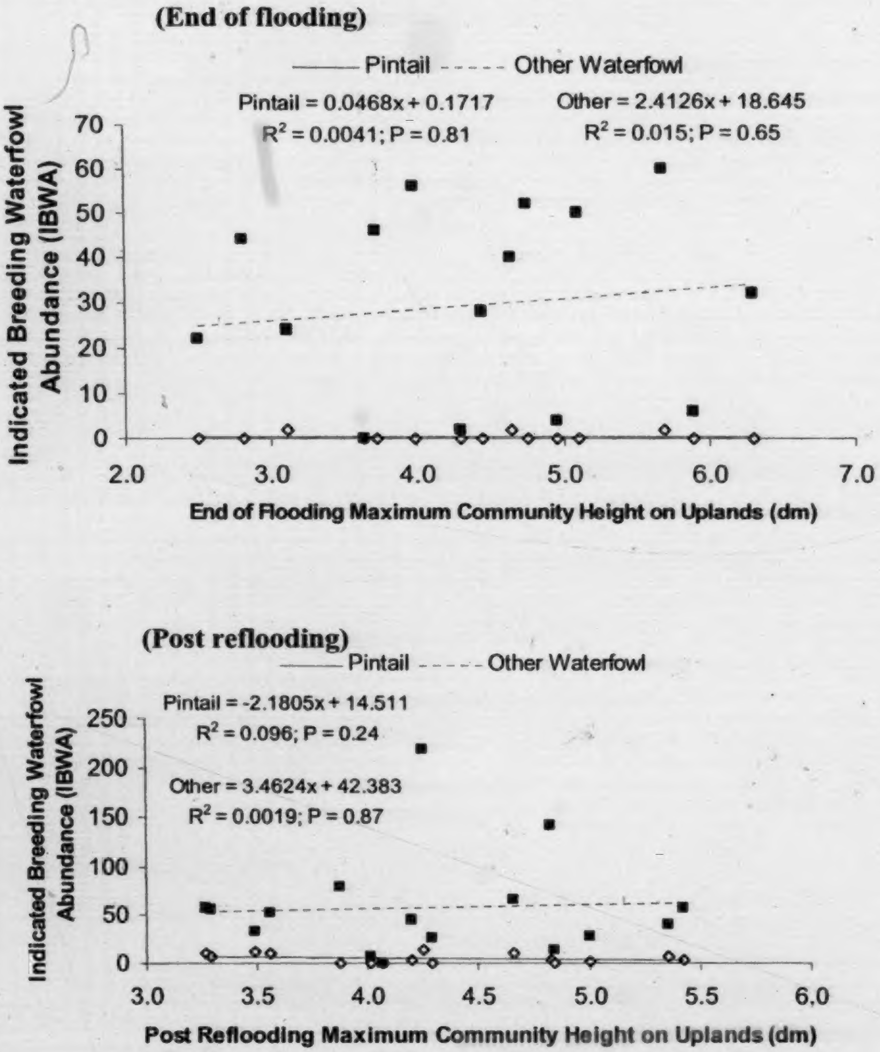
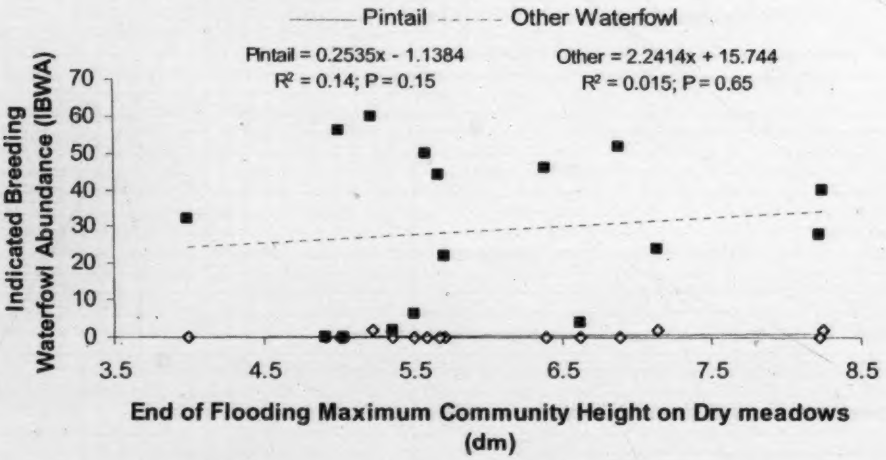


Fig. 6.6: Relationships of IBWA of Pintail and Other Waterfowl to Upland Maximum Community Height during end of flooding treatment and post reflooding sampling periods at Kitsim.

(End of flooding)



(Post reflooding)

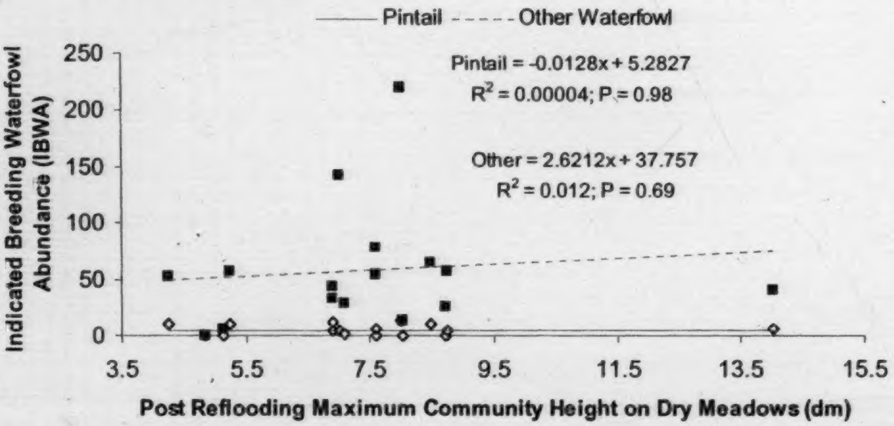


Fig. 6.7: Relationships of IBWA of Pintail and Other Waterfowl to Dry Meadow Maximum Community Height during end of flooding treatment and post reflooding sampling periods at Kitsim.

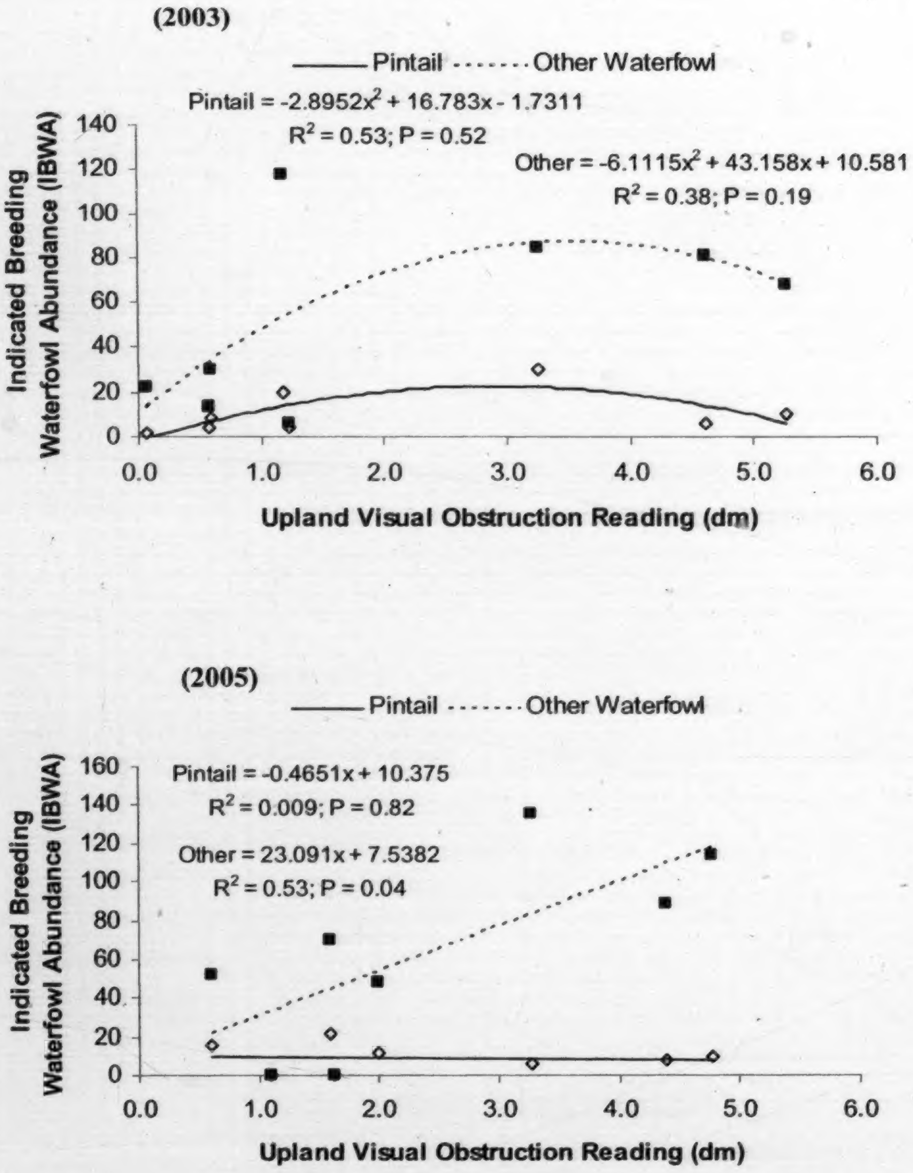


Fig. 6.8: Relationships of IBWA of Pintail and Other Waterfowl to Upland Visual Obstruction Reading at Contra-Costa in 2003 and 2005.

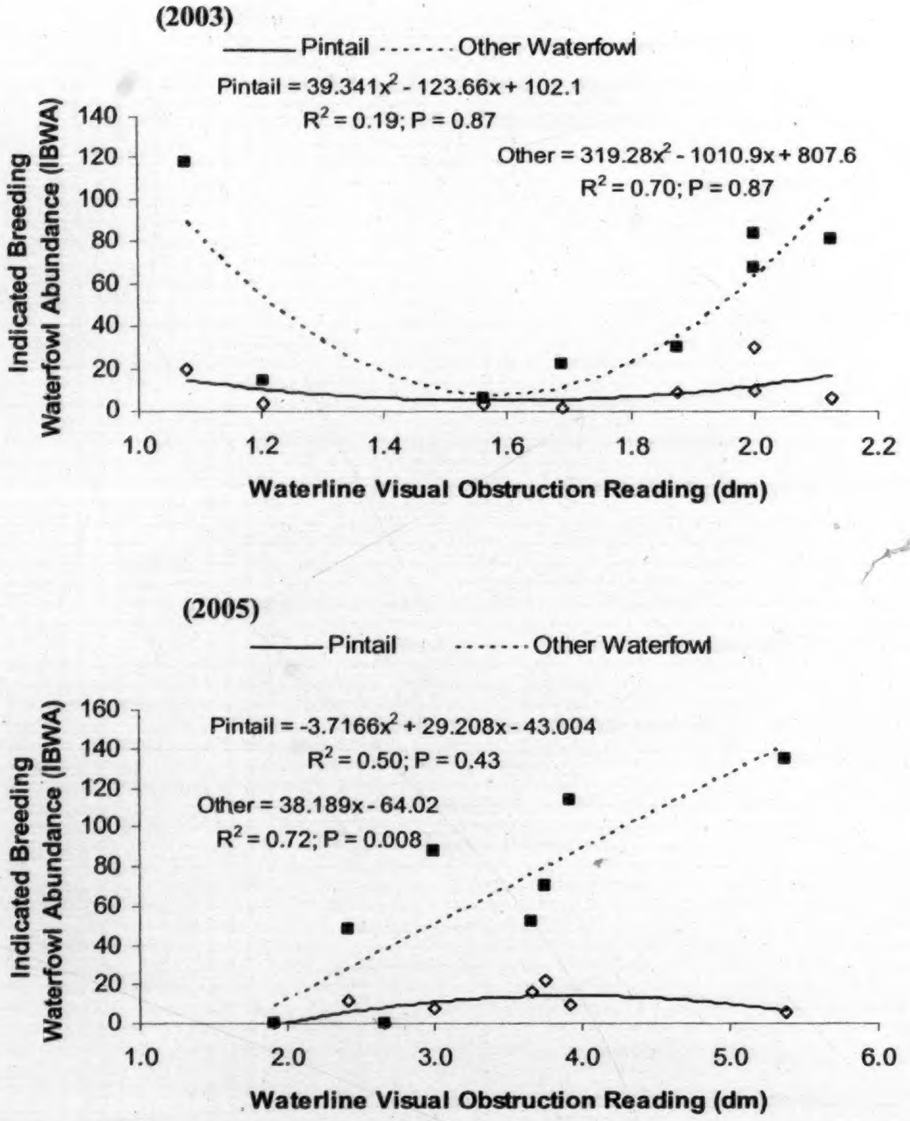
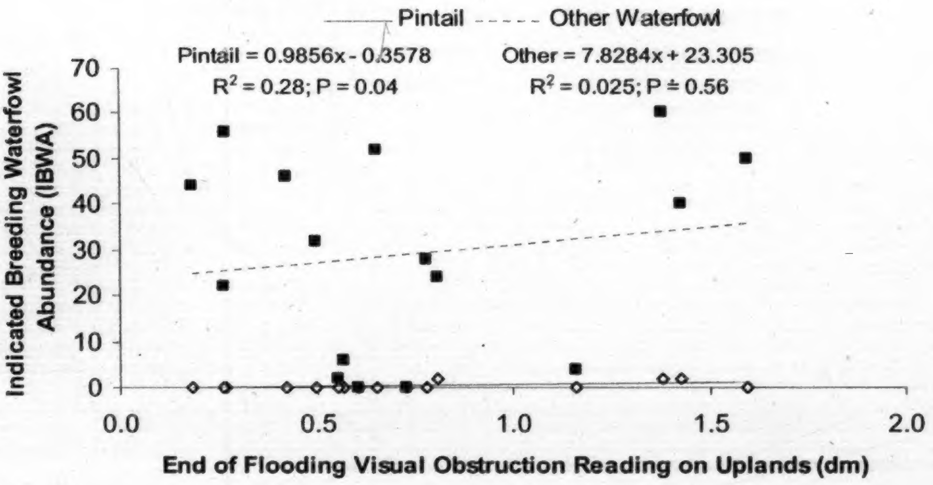


Fig. 6.9: Relationships of IBWA of Pintail and Other Waterfowl to Waterline Visual Obstruction Reading at Contra-Costa in 2003 and 2005.

(End of flooding)



(Post reflooding)

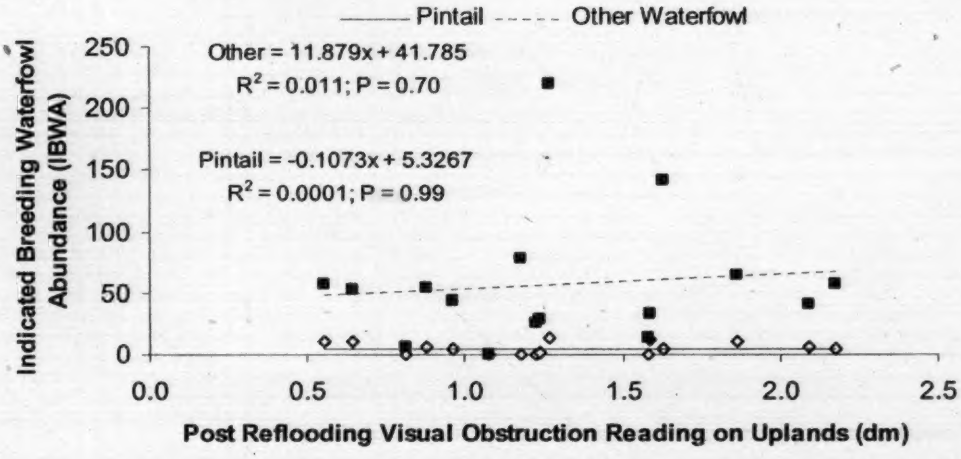
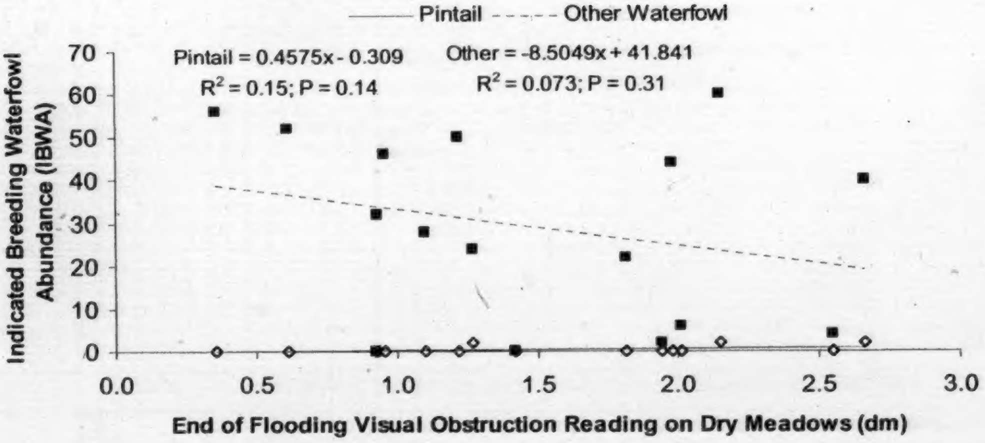


Fig. 6.10: Relationships of IBWA of Pintail and Other Waterfowl to Upland Visual Obstruction Reading during end of flooding treatment and post reflooding sampling periods at Kitsim.

(End of flooding)



(Post reflooding)

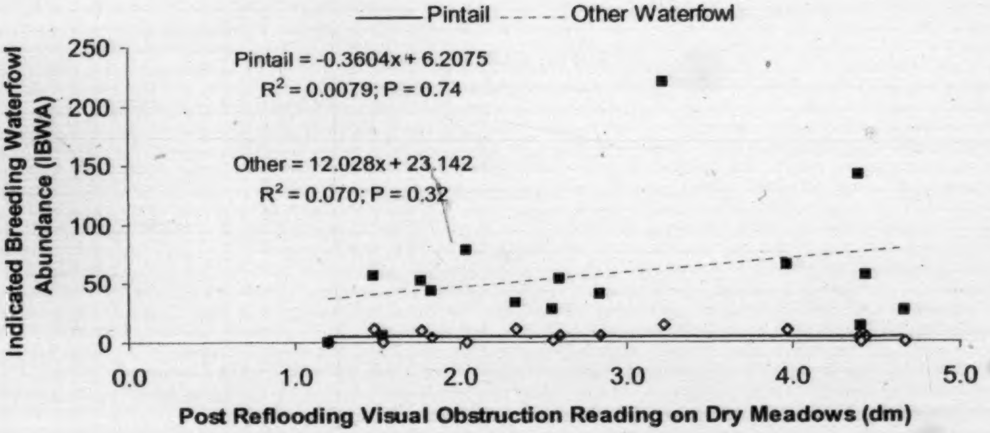


Fig. 6.11: Relationships of IBWA of Pintail and Other Waterfowl to Dry Meadow Visual Obstruction Reading during end of flooding and post reflooding sampling periods at Kitsim.

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CHAPTER 7

SYNTHESIS

7.1. Wetland Development in the Dry Mixed Grass Prairie

The North American Waterfowl Management Plan (NAWMP 1986) has recognized that breeding populations of many species of waterfowl have sharply declined in the Canadian Prairies over the last 50 years. Current breeding populations of many waterfowl continue to remain far below the NAWMP population management goals (Wilkins and Otto 2006). Population declines have been associated with accelerated loss of primary breeding and nesting habitats due to intensified crop agriculture (Boyd 1985, Millar 1989, Nudds and Clark 1993, Podruzny et al. 2002) and extended drought (Johnson and Grier 1988, Williams et al. 1999, Nudds 1983) in the Canadian Prairies. Wetland habitat restoration and enhancement may help increase waterfowl productivity in regions where waterbodies are limited in abundance, as well as benefit other wildlife species and land use.

To restore breeding populations of waterfowl, particularly Northern Pintail in the Canadian Prairies, Ducks Unlimited Canada has undertaken projects to artificially flood natural meadows in the Dry Mixed Grass Prairie region of southeastern Alberta (Sankowski et al. 1987). Initial results of these projects proved to be very successful, and accounted for increased productivity of Northern Pintail (Sankowski et al. 1987). However, the longer-term management of these created wetlands has also presented critical challenges. Vegetation within wetlands created over two decades ago has undergone substantial successional change including the development of near monotypic cattail (*Typha latifolia*) stands (Fig. 7.1). Moreover, a lack of knowledge and understanding of the potential impacts of anthropogenic flooding on successional dynamics of rangeland plant communities has precluded the implementation of flooding regimes necessary for the maintenance of desired native plant communities such as spikerush (*Eleocharis palustris*). Although wetlands dominated by the latter species developed with initial flooding, they have been subsequently replaced by *T. latifolia*. These trends highlighted the need to understand the initial flooding regimes, such as the timing and depth of flooding, necessary to facilitate the establishment and maintenance of *E. palustris* within newly created wetlands, if possible. In addition, the need was apparent to understand the combined effects of anthropogenic flooding and cattle grazing common in the area on subsequent plant community development and associated waterfowl (particularly Northern Pintail) habitat quality. Information on the potential of hydrologic treatments to change *T. latifolia* communities to that of *E. palustris* would aid in improving the quality of habitats for various land uses, including waterfowl and livestock grazing. Overall, clearly established prescriptions for the factors regulating wetland vegetation succession and associated waterfowl and livestock use will help in the development of improved management systems consistent with maintaining the benefits of created wetlands in the Dry Mixed Grass Prairie.

To understand plant community dynamics and address issues of management concern, a four year field study was initiated within native Dry Mixed Grass Prairie rangelands of the Eastern Irrigation District near Brooks, Alberta in August 2002. In order to explore the specific response of *T. latifolia* and *E. palustris* to the planned hydrologic regimes, a preliminary experiment was conducted under greenhouse conditions (Chapter 3) to determine the ability of moisture stress to induce mortality in *T.*

latifolia. A complementary field study evaluated plant community responses along a flooding gradient (i.e., catena topo-sequence) to spring and fall seasons of flood augmentation during new wetland development (Chapter 4). A second field study assessed plant community changes within older established wetlands already dominated by *T. latifolia*. The dynamics of environmental variables (e.g., soil moisture and nutrients) with potential effects on plant community succession were also assessed in Chapter 4. To quantify the potential benefits of created wetlands for land uses other than wildlife, herbage availability, quality and cattle utilization patterns were assessed along hydrologic gradients in Chapter 5. Finally, breeding waterfowl and habitat responses to wetlands subjected to the various flooding treatments were evaluated in Chapter 6. Information from all these assessments is being drawn on to make recommendations on the type of flooding regimes and environmental conditions necessary to maintain desired plant communities such as *E. palustris*, minimize *T. latifolia* encroachment and enhance habitat for waterfowl, particularly Pintail.

7.2. Information Needs for Prairie Wetland Development and Management

Results from Chapter 3 established that *T. latifolia* is less susceptible to soil moisture stress compared to *E. palustris*, and this has important implications on the use of anthropogenic flooding to manage these two important species on created wetlands in the Dry Mixed Grass Prairie of southeastern Alberta, Canada. Although *T. latifolia* is very resistant to drought stress, extended periods of soil drying should be capable of controlling this species. Achieving dry soil conditions with soil moisture ≤5 % for several weeks caused significant *T. latifolia* root mortality. Unfortunately, the minimum field moisture levels attained through two years of flood cessation in the wet meadow and deep marsh zones at Kitsim (established wetland study location) were 13.8 and 21.7%, respectively, well above the required moisture threshold of 5%. These results suggest it is relatively unlikely that *T. latifolia* can be controlled, much less eradicated, from affected wetlands with only two years of flood cessation. However, it should be noted that above normal precipitation during the years of drying also served to counteract attempts to induce moisture stress, thereby enabling *T. latifolia* to tolerate the change in growing conditions. In contrast, *E. palustris* was found to be more susceptible to soil drying based on the greenhouse study. Although *E. palustris* is clearly a highly opportunistic species, rapidly responding to newly initiated flooding, this species was intolerant of extremes in moisture conditions, including deep flooding and excessive drought. Extended flooding at Kitsim also appeared to limit *E. palustris* growth through the invasion of *T. latifolia* and subsequent competitive displacement.

Chapter 4 also revealed that anthropogenic flood augmentation and flood cessation are important disturbance regimes that may affect plant community succession within created wetlands of the Dry Mixed Grass Prairie. Initial flood augmentation caused temporal declines in native species diversity and richness in lower topographic zones and led to the rapid development of monotypic stands dominated by *E. palustris*. Although it was expected that high levels of anthropogenic flooding might facilitate exotic invasion into the native ecosystems associated with these newly developed wetlands (Wilcox and Thurow 2006), results of recent flooding at Contra-Costa did not support this view. Instead, the initial development of monotypic *E. palustris* communities appeared to prevent exotic invasion in lower topographic zones.

With respect to soil nutrients on newly developed wetlands at Contra-Costa, season of flooding was found to have little effect on levels of soil available nutrients, including nitrate, ammonium and phosphate. Nutrient data at Contra-Costa indicated that ammonium replaced nitrates within flooded lower topographic zones, with ammonium levels temporally declining with repeated annual flooding. Soil available phosphorus, on the other hand, demonstrated strong spatial increase towards the lower topographic zones, and in particular, increased in accumulation with repeated annual flooding. Notably, *T. latifolia* has been reported to utilize nutrient enrichment (particularly elevated phosphorus) as a mechanism for competitively displacing less aggressive plant communities from wetlands (Newman et al. 1996, Weng et al. 2006). Nutrient data in landscapes associated with newly developed wetlands at Contra-Costa supported this assertion (Chapter 4). Under extended annual flooding, the temporal increases in phosphorus in lower topographic positions are likely to combine with increased soil moisture to facilitate *T. latifolia* invasion and to the displacement of *E. palustris*. Notably, *E. palustris* demonstrated a surge in growth following initial flooding. This finding leads to the supposition that *E. palustris* responded to the high initial ammonium levels arising from reduced soil conditions under flooding (Rejmankova et al. 1995, Mitsch and Gosselink 2000, Sorrell et al. 2002), which it subsequently utilized, leading to ammonium depletion with continued annual flooding in subsequent years. However, the initial surge in *E. palustris* growth did not prevent encroachment by *T. latifolia*, which was found later on in newly developed wetlands at Contra-Costa, likely in response to increasing phosphorus accumulation (Weng et al. 2006). However, little evidence was found for rapid *T. latifolia* expansion under the flooding regime tested here, providing optimism that *T. latifolia* abundance may be kept at low levels with careful anthropogenic flood management in recently established wetlands. Thus, more information is clearly needed on the specific flood regime (i.e., frequency, depth and duration of flooding) that will limit *T. latifolia* invasion and expansion within these newly developing wetlands of the Dry Mixed Grass Prairie.

Within *T. latifolia* dominated established wetlands at Kitsim, fall and spring flooding produced similar effects to one another, very different from that of newly developed wetlands at Contra-Costa. Neither of these treatments was capable of controlling, or decreasing for that matter, *T. latifolia* within the deep marsh zones. Instead, these flooding treatments led to the maintenance of a more stable *T. latifolia* community to the exclusion of other vegetation. While one year of flood cessation was less effective in inducing changes in *T. latifolia* communityies at Kitsim, two years of flood cessation reduced the relative abundance of *T. latifolia* to a greater extent in the shallow and deep marsh zones of affected wetlands, and subsequently led to increased diversity and richness of both native and introduced species (Chapter 4). Notably, *T. latifolia* community change did not coincide with the development of the desired *E. palustris* community, and instead increased the abundance of introduced species, including noxious weeds. Furthermore, subsequent reflooding resulted in *T. latifolia* return, though in less abundance compared to wetlands flooded annually in fall or spring, highlighting the resilience of *Typha* communities to reductions in soil moisture.

Soil nutrient dynamics at Kitsim indicated that flood cessation generally led to a reduction in the levels of soil available nitrate and ammonium, especially in lower topographic zones. However, levels of these nutrients promptly increased with subsequent reflooding. In contrast, flood cessation led to a temporal increase in phosphate levels, which declined with reflooding. Thus, while flood cessation limits nitrogen accumulation and *T. latifolia* growth in affected wetlands, it may also lead to a reduction in phosphorus uptake because of greater *T. latifolia* mortality.

In addition to flood cessation, cattle grazing affected the relative abundance of many important native and introduced forage species at Kitsim, suggesting these two disturbances must be managed together while assessing the condition of plant communities. Individual plant species abundance varied in response to the presence and absence of cattle grazing across topographic positions of flood cessation wetlands. For example, grazed areas had greater abundance of *A. smithii, C. filifolia, A. pectiniforme, E. glandulosum*, *H. jubatum*, *P. palustris* and *C. arvense*, but a reduction in the relative abundance of *S. comata, P. pratensis* and *S. arvensis*. An important observation is that cattle grazing impacted plant species to a greater extent in lower topographic zones of flood cessation wetlands. In particular, grazed areas at that location had greater abundance of mesic wetland plants like *R. occidentalis*, but less of hydric species such as *E. palustris* and *T. latifolia*. Species that increased under cattle grazing were mostly unpalatable herbage species. On the other hand, species such as *S. comata, P. pratensis, E. palustris* and *S. arvensis* appeared very palatable to cattle, and hence experienced a significant reduction under cattle grazing. Although *T. latifolia* is not a highly preferred forage, cattle grazing appeared to cause a significant reduction in its relative abundance, and may therefore hold promise for use as a control method alongside flood cessation.

Results of Chapter 5 indicated that herbage production across the landscape of affected wetlands may be enhanced with artificial flooding in Dry Mixed Grass Prairie, and may concentrate livestock use in these areas. However, herbage components were spatially variable and levels of biomass production and quality varied markedly depending on the flooding treatment and depth of flooding.

On newly developed wetlands at Contra-Costa, while grass biomass and crude protein yield (CPY) levels were greater on upper topographic zones, those of *Eleocharis* increased towards the lower topographic zones. Overall, total CPY was greatest in the lower three topographic zones and cattle were found to maximize forage intake, especially *Eleocharis* in lower topographic zones, making such topographic zones important for cattle production in the Dry Mixed Grass Prairie. However, cattle uniformly utilized the entire landscape as a result of herbage availability across all topographic positions, indicating that the entire landscape associated with created wetlands are important as a source of forage for range cattle production.

At Kitsim, where *T. latifolia* dominated the established wetlands, the production and quality of various herbage components were also temporally variable, depending heavily on the type of artificial flooding (or drying) treatment and natural rainfall patterns. While flood cessation was capable of reducing *T. latifolia* production on affected wetlands, *E. palustris* was susceptible to flood cessation, further impacting foraging opportunities for livestock. Although *T. latifolia*-infested wetlands had high CPY levels, cattle displayed limited use of *T. latifolia*, rendering such wetlands of less economic importance for cattle production.

Finally, assessment of flooding treatment effects on waterfowl use in Chapter 6 indicated that anthropogenic flooding is important for enhancing waterfowl production in Dry Mixed Grass Prairie environments. Wetland availability in spring proved to be a critical determinant of the abundance of breeding waterfowl on the prairie landscape, particularly Pintails. Overall, compared to natural flooding from snow melt and precipitation, anthropogenic flooding in either fall or spring increased Pintail abundance on newly developed wetlands at Contra-Costa. Furthermore, spring flooding led to a greater increase in Pintail abundance compared to fall flooding. The abundant Pintail numbers on newly developed wetlands may be due to food availability (Bataille and Baldassarre 1993).

Unlike Pintails, Other Waterfowl at Contra-Costa consistently favored fall wetlands compared to spring. Fall wetlands had moderately higher vegetation structure, including height and visual obstruction, especially in the sub-irrigated upland and waterline zones, leading to the supposition that moderately tall and dense vegetation in riparian zones around wetlands in the Dry Mixed Grass Prairie has critical implications on the abundance of Other Waterfowl. Overall, Pintail abundance at Contra-Costa represented only 14.2% of Other Waterfowl on new fall wetlands, and 23% on new spring wetlands.

Both Pintail and Other Waterfowl utilized the flood cessation wetlands at Kitsim, although Pintail was more susceptible to flood cessation. Notably, flood cessation wetlands were at least 25% flooded (by area) during the spring of each census year as a result of moisture recharge during snowmelt, and wetland moisture availability remains the key factor regulating waterfowl use of wetlands.

Results of this study also indicated wetland size and vegetation characteristics to be important predictors of wetland use by Pintail and Other Waterfowl. Generally, wetland size appeared to influence Pintail abundance, as Pintails had a greater affinity for small wetlands (less than 5 ha) in the Dry Mixed Grass Prairie. This is likely because smaller wetlands are shallow, ranging from ephemeral to semi-permanent types, and are interspersed with short structured vegetation typically preferred by Pintails (Kaminski and Prince 1984, Kaminski and Weller 1992). Other Waterfowl, on the other hand, had greater tolerance for larger wetlands (up to about 8 ha at Contra-Costa with no specific upper limit at Kitsim), potentially because of the wide range of habitat requirements and foraging opportunities for the various species included as Other Waterfowl.

Wetland moisture availability also affected the structure (MCH) and density (VOR) of vegetation associated with all study wetlands at Contra-Costa and Kitsim. Spatial variation typically reflected lower values on uplands, to the greatest vegetation structure in low lying topographic zones of most flooding treatments. The dynamics of both Pintail and Other Waterfowl abundance in response to flooding treatments paralleled those of MCH and VOR, highlighting the importance of riparian vegetation structure in affecting waterfowl abundance in the Dry Mixed Grass Prairie. Thus, soil moisture gradients across the landscape appear critical in dictating the structure and density of vegetation along wetlands, and consequently, the abundance of Pintail and Other Waterfowl. In addition, among the vegetation structure and density measurements assessed, MCH was found to be sensitive in detecting changes in waterfowl abundance, although MCH appeared to be a poor predictor of waterfowl abundance. Instead, waterfowl abundance was more strongly correlated with VOR, suggesting that where comprehensive VOR data are available, they may be a better predictor of Pintail and Other Waterfowl abundance on wetlands in the Dry Mixed Grass Prairie.

At Kitsim, areas exposed to cattle grazing had lower MCH and VOR compared to those excluded from grazing, particularly in dry and wet meadows. Grazing has been described as an important disturbance regime that significantly impacts herbage availability in lower topographic zones associated with riparian wetlands (Willms 1988, Asamoah et al. 2003). The reduction in MCH and VOR in grazed wet and dry meadow zones in the study suggests that herbage removal through cattle grazing affected both the structure and density of vegetation at these locations. Consequently, a combination of flood cessation and cattle grazing have the potential to reduce tall and dense vegetation, which otherwise may remain unsuitable as habitat for Pintail and Other Waterfowl.

7.3. General Conclusions, Limitations and Future Direction

The present study has improved our understanding of the effects of wetland development on plant community dynamics and utilization patterns along hydrologic gradients in the Dry Mixed Grass Prairie (Fig. 7.1). It has identified potential uses and limitations of hydrologic manipulation for modifying vegetation communities through succession and control of *T. latifolia* in the region. Although this study was conducted under stochastic environmental conditions, including above-normal precipitation from 2003 to 2005, the results of the greenhouse and field experiments emphasized the relative susceptibility and resistance of *E. palustris* and *T. latifolia*, respectively, to soil moisture stress. Both experiments revealed *E. palustris* to be more susceptible to changes in soil moisture compared to *T. latifolia*, with the latter being very difficult to control using induced moisture stress. Furthermore, once *E. palustris* has been completely displaced by *T. latifolia* on well established wetlands, and two years of flood cessation has been used to reduce the relative abundance of *T. latifolia, E. palustris* is less likely to be restored immediately after reflooding. Thus, in order to minimize *T. latifolia* invasion and colonization of newly developed wetlands, it is suggested that annual anthropogenic flooding should be interspersed with periodic flood cessation.

Based on the current study, more than 2 years of flood cessation may be required to control *T. latifolia* within established wetlands of the Dry Mixed Grass Prairie. These hydrologic manipulations may either enhance habitats for Pintail and Other Waterfowl, such as the case with initial flooding, or cause adverse effects, depending on the intensity and frequency of flooding and/or drying. While flood cessation may help control *T. latifolia*, it also results in an associated tradeoff through short-term reductions in waterfowl production, with reflooding reversing this decline and leading to increased Pintail and Other Waterfowl abundance. Thus, while short-term habitat modification such as flood cessation intended to control undesirable plant communities such as *T. latifolia* may initially cause adverse effects on prairie breeding waterfowl, especially Pintail, subsequent improvements in waterfowl abundance may occur. Enhanced habitat with flood modification may justify the use of 2 year or longer drying treatments to achieve the soil moisture thresholds necessary to reduce *T. latifolia*.

Due to time constraints, this study did not examine longer-term hydrologic treatment effects, which may have identified the drought /soil moisture threshold under field conditions needed to more effectively control *T. latifolia* in affected wetlands of the Dry Mixed Grass Prairie. In addition, the relatively short-term study period could not evaluate *E. palustris* recovery in drought-stressed wetlands previously dominated by *T. latifolia*. More information is needed on the effects of longer-term drying treatments as a method of *T. latifolia* control, including the additive role of natural droughts in this process. Within newly established wetlands, further information is needed on the fluctuations in moisture needed to prevent *T. latifolia* from reaching threshold abundances where this species may be able to rapidly expand and colonize created wetlands. For example, infrequent drying may be capable of minimizing *T. latifolia* in new wetlands, while long-term drying may be required to restore more open, low-structured *E. palustris* communities in situations where liberal floodwater addition has allowed for shifts to *T. latifolia* domination.

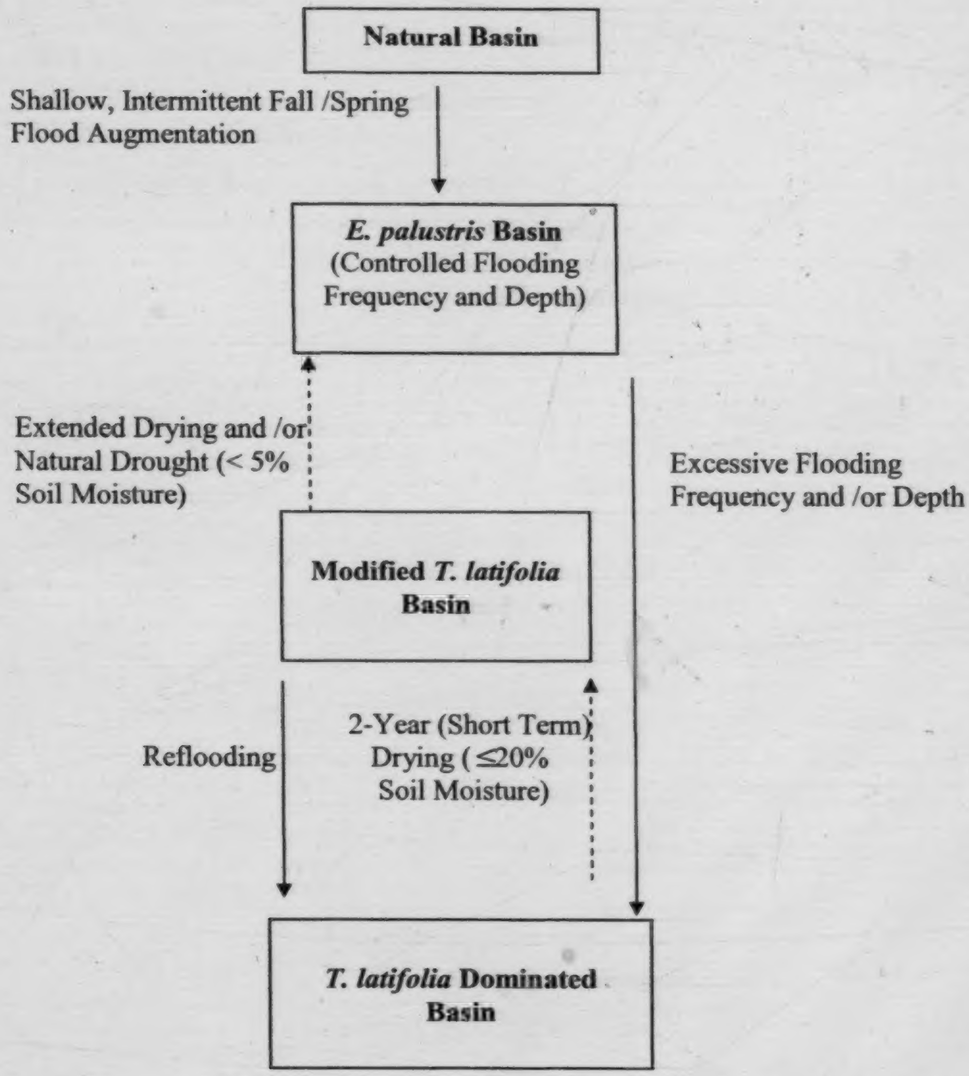
Natural Basin
Shallow, Intermittent Fall /Spring Flood Augmentation
E. palustris Basin (Controlled Flooding Frequency and Depth)
Extended Drying and /or Natural Drought (< 5% Soil Moisture)
Excessive Flooding Frequency and /or Depth
Modified T. latifolia Basin
Reflooding
2-Year (Short Term) Drying (≤20% Soil Moisture)
T. latifolia Dominated Basin

Fig. 7.1: Schematic state-and-transition model indicating the successional dynamics of *E. palustris* and *T. latifolia* in response to anthropogenic flood augmentation and flood cessation in the Dry Mixed Grass Prairie of southeastern Alberta

7.4. References

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APPENDICES

Appendix I: Mean Monthly Precipitation at Brooks in the Dry Mixed Grass Prairie of southeastern Alberta, Canada.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2005												
Rain	0	0	0	15.3	13.6	214.3	42.4	87.2	97	30.6	8.2	3
Snow	13.2	1.4	15.3	0.6	0	0	0	0	0	0	5.6	4
Total	9.8	1.4	6.8	15.9	13.6	214.3	42.4	87.2	97	30.6	13.8	7
2004												
Rain	0	0	2.8	13.6	36.4	64.8	37.6	67	8.6	9	1.1	3.6
Snow	32	1.3	3.9	0	0.7	0	0	0	0	5.3	0.7	11
Total	32	1.3	6.7	13.6	37.1	64.8	37.6	67	8.6	14.3	1.8	14.6
2003												
Rain	0	0	0.6	25.8	27.7	59	9.4	13.4	35.3	8.8	1	0
Snow	5.5	11.1	4.1	4.3	15.6	0	0	0	0	24.9	17.7	3
Total	5.5	11.1	4.7	30.1	43.3	59	9.4	13.4	35.3	33.7	18.7	3
2002												
Rain	2.4	0	0	4.2	5.6	111.6	23.2	53.4	52.8	4.4	0	0
Snow	11	12.4	31.2	0.8	12.2	0	0	0	2	7.7	7	4.6
Total	13.4	12.4	29.9	5	17.8	111.6	23.2	53.4	54.8	12.1	7	4.6
2001												
Rain	0	0	2.6	9.9	9.6	42.8	13.8	1.4	16.6	8.4	0	0.6
Snow	8.3	42.9	10.4	10.4	0	0	0	0	0	0	10.9	2.8
Total	8.3	42.9	13	20.3	9.6	42.8	13.8	1.4	16.6	8.4	10.9	3.4
1971-2000*												
Rain	1.1	0.6	2.7	20.2	42.6	58.8	41.7	39.3	38.9	11.5	2	0.9
Snow	14.9	12.8	17.9	8	1.5	0	0	0	0.5	5.5	14	20.3
Total	14.7	12.2	19.5	27.9	44.1	58.8	41.7	39.3	39.4	17	14.7	18.9

Appendix II: Mean Monthly Temperatures (°C) at Brooks in the Dry Mixed Grass Prairie of southeastern Alberta, Canada.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
2005												
Mean Max	-6.6	4.8	8	14.2	19.1	19.8	25.6	23	18.5	14.1	6.8	-0.2
Mean Min	-18.5	-10.9	-6.6	-1.6	3.3	9	10.9	8.2	4.3	-0.8	-5.9	-10.8
Mean Temp	-12.6	-3.1	0.7	6.3	11.2	14.4	18.2	15.6	11.4	6.7	0.4	-5.5
2004												
Mean Max	-8.6	-1.7	7.4	15.2	16.3	21.2	26	23.4	18.4	12.2	8.2	0.3
Mean Min	-16.9	-13.1	-4.1	-1.5	2.6	7.3	11.1	9.9	3.7	-2.7	-6.9	-12.8
Mean Temp	-12.8	-7.5	1.7	6.9	9.5	14.3	18.6	16.7	11	4.8	0.7	-6.3
2003												
Mean Max	-2.8	-3	2.8	12.7	16.4	21.8	28.4	28.6	19.1	15.9	-2.5	-1.7
Mean Min	-14.6	-14.9	-9.7	-0.1	3.1	9	11.1	11.8	4.8	0.7	-15.6	-11.9
Mean Temp	-8.7	-8.9	-3.5	6.3	9.8	15.5	19.8	20.2	12	8.3	-9.1	-6.8
2002												
Mean Max	-1.7	3.7	-6.4	9.3	17.2	22.8	28.1	22.9	18.6	7.6	7.7	2.7
Mean Min	-13.9	-10.2	-20.1	-4.6	1.9	9.5	11.6	9	5.2	-3.6	-5.5	-11.6
Mean Temp	-7.8	-3.3	-13.3	2.3	9.6	16.2	19.9	16	12	2	1.1	-4.5
2001												
Mean Max	3.1	-6.1	8	13.3	21.3	22.6	27.8	29.8	22.8	13	7.5	-3.5
Mean Min	-10.5	-20.7	-5.6	-2.3	4.8	8.3	11.9	10.2	5.7	-2.6	-4.3	-15.1
Mean Temp	-3.7	-13.4	1.2	5.5	13.1	15.5	19.9	20	14.3	5.2	1.6	-9.3
1971-2000*												
Mean Max	-5.6	-2.7	3.7	12.7	18.9	23.1	25.7	25	18.8	13.6	1.9	-4.2
Mean Min	-17	-14.1	-7.8	-1.7	4.2	8.8	10.9	9.7	4.2	-1.1	-9.7	-15.7
Mean Temp	-11.3	-8.4	-2.1	5.5	11.6	16	18.3	17.4	11.5	6.3	-4	-9.9
SD	5.6	5.5	3.2	2.6	1.5	1.5	1	2	1.9	1.6	4.2	5.2

Appendix III: Schedule of artificial flooding treatments implemented on new study wetlands at Contra-Costa to examine new wetland development in the Dry Mixed Grass Prairie.

Wetland		Flooding	2002	2003		2004		2005
Basin	Size	Treatment[1]	Fall	Spring	Fall	Spring	Fall	Spring
Con-A	4.2	FF	flood		flood		flood	
Con-B	3.7	SF		flood		flood		flood
Con-C	3.1	SF		flood		flood		flood
Con-D	7.0	FF	flood		flood		flood	
Con-E	7.3	FF	flood		flood		flood	
Con-F	7.5	FF	flood		flood		flood	
Con-G	2.5	NF	n/a	n/a	n/a	n/a	n/a	n/a
Con-H	2.1	NF	n/a	n/a	n/a	n/a	n/a	n/a

[1] FF, SF and NF represent fall flooding, spring flooding and natural (no artificial) flooding, respectively.

Appendix IV: Schedule of flooding treatments implemented on well-established *T. latifolia*-dominated wetlands at Kitsim. The four wetlands selected for the 2YNF treatment were last flooded in fall 2001, which was considered the initial pre-treatment flooding date for these. Pre-treatment flooding for all remaining wetlands was implemented in fall 2002.

Wetland Basin			Flooding Treatmen[1]	2002	2003		2004		2005
EID Label	Study Label	Size		Fall	Spring	Fall	Spring	Fall	Spring
B4	Kit-A	9.4	1YNF	flood		no flood		flood	
B7	Kit-B	9.1	1YNF	flood		no flood		flood	
B11	Kit-C	16.6	2YNF	no flood		no flood		flood	
B9b	Kit-D	6.3	SF	flood		no flood	flood		flood
B20a	Kit-E	14.9	FF	flood		flood		flood	
B20a	Kit-F	14.9	FF	flood		flood		flood	
B20b	Kit-G	5.0	1YNF	flood		no flood		flood	
B23	Kit-H	3.3	1YNF	flood		no flood		flood	
A9a	Kit-I	9.6	SF	flood		no flood	flood		flood
A9b	Kit-J	9.2	SF	flood		no flood	flood		flood
A7	Kit-K	13.6	2YNF	no flood		no flood		flood	
A5	Kit-L	12.1	SF	flood		no flood	flood		flood
A7	Kit-M	13.6	2YNF	no flood		no flood		flood	
CA6	Kit-N	14.2	FF	flood		flood		flood	
CA6	Kit-O	14.2	FF	flood		flood		flood	
D18	Kit-P	7.8	2YNF	no flood		no flood		flood	

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[1] FF, SF, 1YNF and 2YNF represent fall flooding, spring flooding, one year no flooding and two years no flooding, respectively.

Appendix V: Season-long changes in flooding depths (cm) of wetland basins following implementation of flooding treatments at Contra-Costa in each of three study years.

Flooding Treatment	2003			2004			2005		
	Early May	Early Jul	Mid Aug	Early May	Early Jul	Mid Aug	Early May	Early Jul	Mid Aug
Natural Flooding	32.5	15	0	35	12.5	0	0	27.5	0
Fall Flooding	70	55	20	77.5	57.5	36.2	50	48.8	21.3
Spring Flooding	60	40	0	77.5	55	32.5	57.5	55	17.5

Appendix VI: Season-long changes in flooding depth class of wetland basins following implementation of hydrologic treatments at Kitsim in each of three study years.

Flooding Treatment[1]	2003			2004			2005 (post-reflood)		
	Early May	Early Jul	Mid Aug	Early May	Early Jul	Mid Aug	Early May	Early Jul	Mid Aug
Fall Flooding	5	3.8	0.3	4.1	3	1	3.9	3.5	1.3
Spring Flooding	5	4	0	4	3	2	4	4	0.8
1YNF	5	3.5	0	1	0	0	2.3	3	1
2YNF	1.5	0.8	0	1	0	0	3.4	1.5	0.5
Upper Reservoir (check)	5	5	3	4	4	3	4	4	4

[1] The 1YNF and 2YNF flooding treatments represent one year of flood cessation and two years of flood cessation, respectively.

Kitsim water depth scores:
0 – completely dry;
1 – between 1 and 25% of basin area flooded;
2 – between 26 and 50% of basin area flooded;
3 – between 51 and 75% of basin area flooded;
4 – between 76 to 100% of basin area flooded;
5 – over 100% of basin area flooded.

Appendix VII: Seasonal changes in wetland water quality, including dissolved oxygen (mg/l), electrical conductivity (μS), salinity (ppm) and pH, total Kjeldahl nitrogen (TKN) (mg/l) and total phosphorus (TP) (mg/l) under three flooding treatments investigated at Contra-Costa during each of three study years.

Water Quality Indicator Flooding Treatment	2003			2004			2005		
	Early May	Early Jul	Mid Aug	Early May	Early Jul	Mid Aug	Early May	Early Jul	Mid Aug
Dissolved Oxygen (8-10am)									
Natural flooding	6.6	2.9		5.9	2.9			4.4	
Fall flooding	7.5	2.5	4.1	6.8	9	4.3	5.7	4.7	3.6
Spring flooding	7.4	1.1		6.5	11.2	4.2	4.3	4.5	3.8
Tilley Reservoir (check)	7.9	7.5					6.7		4.2
Conductivity (specific)									
Natural flooding	135	121		94	76.1			77	
Fall flooding	354	473	804	368	444	560	547	438	53
Spring flooding	446	404		450	510	430	724	428	9
Tilley Reservoir (check)	453	544					437		257
Salinity									
Natural flooding	0.1	0.1		0.1	0			0	
Fall flooding	0.2	0.2	0.4	0.2	0.2	0.3	0.2	0.2	3.2*
Spring flooding	0.2	0.2		0.2	0.3	0.3	0.4	0.2	5.2*
Tilley Reservoir (check)	0.2	0.3					0.2		0.1
pH									
Natural flooding	5.5	5		5	5				
Fall flooding	6.2	6.4	6.7	6.1	7.9	7.9	6.9	6.8	5.7
Spring flooding	6.3	6		6	6.8	6	6	6	4.5
Tilley Reservoir (check)	6.5	8					6		6
TKN									
Natural flooding		4.3		2.5	3			7.8	
Fall flooding		5.8		1.7	4.6		2.3	5.1	
Spring flooding		3.3		1.7	4.2		3	5	
Tilley Reservoir (check)				0.8	0.5		0.4	0.7	
TP									
Natural flooding		1.3		0.9	2			2.9	
Fall flooding		1.7		0.5	1.3		0.4	1.1	
Spring flooding		1.2		0.5	1.4		1.2	1.2	
Tilley Reservoir (check)				0.1	0.1		0.1	0.1	

Appendix VIII: Seasonal changes in wetland water quality, including dissolved oxygen (mg/l), electrical conductivity (µS), salinity (ppm) and pH under four hydrologic regimes investigated at Kitsim during each of three years of study.

Water Quality Indicator Flooding Treatment	2003			2004	2005 (post-reflood)		
	Early May	Early Jul	Mid Aug	Early May	Early May	Early Jul	Mid Aug
Dissolved Oxygen (8 - 10 am)							
Fall flooding	5	1.5	6.5	5.5	4	3.9	3.8
Spring flooding	5.2	2.6		8.9	4.7	1.4	2.5
One year drying	6.8	2.4			3.8	4.9	36
Two years drying	5.9	7.3			5.1		2.9
Upper Reservoir (check)	8.8	9.9			5.6		
Conductivity (specific)							
Fall flooding	719.6	760.8	789.4	667.3	990.1	1253.6	406.9
Spring flooding	476.5	590.3		609.2	714.6	664	339.3
One year drying	536.5	696.7			853	596	515.5
Two years drying	976.4	1217			1004.2	697.4	
Upper Reservoir (check)	408.8	371.7			53		
Salinity							
Fall flooding	0.4	0.4	0.1	0.3	0.5	0.6	0.2
Spring flooding	0.2	0.3		0.3	0.4	0.4	0.2
One year drying	0.3	0.3			0.4	0.3	0.3
Two years drying	0.5	0.7			0.5	0.4	
Upper Reservoir (check)	0.2	0.2			0.3		
pH							
Fall flooding	6.1	6.3	7.9	6.3	6.4		6.7
Spring flooding	6	6.5		6.8	6.9		6.5
One year drying	6.3	7.1			6.8		7.6
Two years drying	6.7	9.3			7.2		6.6
Upper Reservoir (check)	6.5	9			6.5		

Appendix IX: Standard ANOVA models used for testing fixed effect factors in the analysis of vegetation data at Contra-Costa and Kitsim.

Contra-Costa (Split-plot design)	Kitsim (Split-plot design)
Covariate (Pre-flooding)	*Covariate (Pre-flooding)*
Flooding Treatment	Flooding Treatment
Topographic Position	Cattle Grazing[1]
Flooding x Position	Flooding x Grazing
Sampling Year	Topographic Position
Year x Flooding	Flooding x Position
Year x Position	Grazing x Position
Year x Flooding x Position	Flooding x Grazing x Position
	Sampling Year[2]
	Year x Flooding
	Year x Grazing
	Year x Position
	Year x Flooding x Grazing
	Year x Flooding x Position
	Year x Grazing x Position
	Year x Flooding x Grazing x Position

[1] Where cattle grazing factor or its interaction with other treatment factors was insignificant ($P > 0.05$), grazing was removed from removed from statistical data analysis models in order to reduce model complexity.

[2] Where cattle grazing factor was retained in analysis models, each sampling year's data was analyzed independently in order to reduce model complexity.

Appendix X: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of upland zones associated with fall flooded wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Upland Zone associated with FF[1] Wetlands at Kitsim

Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre[2]	End	Post
	Canopy Cover (%)					
Achillea millefolium	0.8	0.8	0.9	0.5	0.5	0.2
Agropyron dasystachum	9.4	3.1				
Agropyron pectiniforme	0.9	0.9	0.2	4.2	2.8	1.7
Agropyron smithii	3.1	1.9	10.6	15.8*	5.5*	8.9
Antennaria parvifolia	0.3					
Artemisia frigida	0.5	4.1	8.8	0.2	3.9	1.9
Artemisia ludoviciana	7.0	0.2		3.8		
Atriplex nuttallii	0.2					
Bouteloua gracilis	0.2	4.7	0.3		5.9	0.9
Bromus inermis				0.5		
Carex filifolia	16.9	13.4	10.9	11.7*	10.2	13.6
Distichlis spicata	14.4	9.2	11.9	12.2	10.5	23.0*
Elymus junceus	12.1	4.5	11.3	12.5	10.0*	7.0*
Erysimum aspermum				0.2		
Gutierrezia sarothrae	0.2		0.5	0.5		
Hordeum jubatum	1.3	1.4	2.5	5.5*	4.4	10.0*
Koeleria macrantha	2.5	0.8	0.6	1.3	0.2	0.2
Opuntia polyacantha		0.3	0.2	0.3		0.3
Phlox hoodii	0.2					
Poa pratensis	8.4	10.0	0.9	10.3	10.5	
Poa sandbergii	1.9	1.1	0.2	5.2*	0.8	0.3
Selaginella densa	3.9	4.4	5.6	6.6	3.4	3.0
Sphaeralcea coccinea	0.3	0.3	0.2			
Stipa comata	0.5	0.3	2.0			
Stipa viridula	1.4		1.7			
Sueada monquinii			4.2			2.5
Thermopsis rhombifolia	0.2	0.2				
Introduced Species						
Sonchus arvensis		0.2				
Taraxacum officinale	0.2					

[1] The FF treatment represents fall flooding.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Appendix XI: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of dry meadow zones associated with fall flooded wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Dry Meadow Zone associated with FF[1] Wetlands at Kitsim

Scientific Name	Ungrazed			Grazed		
	Pre[1]	End	Post	Pre[1]	End	Post
	Canopy Cover (%)					
Native Species						
Achillea millefolium		0.5		0.8	0.8	0.5
Agropyron smithii	2.3	4.5	3.0	3.1	2.7	2.3
Agrostis scabra		0.2			0.5	
Beckmannia syzigachne		0.2		0.3		
Bouteloua gracilis					1.7	
Carex rostrata	3.1	2.2	3.6	7.7*	4.7	2.7
Deschampsia caespitosa	1.3	1.6	1.9	0.2	0.3	0.2
Distichlis spicata	2.5	1.4	4.4	14.4*	4.5	12.2*
Erigeron pumulis			0.2		4.2	4.2
Eleocharis palustris	2.0	0.8		1.4		0.2
Erysimum aspermum			0.2	0.2		
Gutierrezia sarothrae				0.2		0.6
Hordeum jubatum	18.4	11.7	4.1	15.0	10.0	7.7
Juncus balticus	2.0	2.2	3.8	0.6		0.3
Mentha arvensis	0.3	3.0	2.0	1.4	0.3	0.5
Opuntia polyacantha			0.3			0.3
Plantago purshii						1.3
Poa palustris	13.6	16.7	10.8	6.4*	4.5*	13.0
Poa pratensis	8.0	7.8	9.2	9.5	15.6*	0.8*
Puccinellia nuttalliana						0.5
Rumex occidentalis	1.6	2.5	3.6	3.0	1.3	
Suaeda monquinii	0.3		0.2			1.4
Introduced Species						
Chenopodium album		2.7	1.6			
Cirsium arvense	1.1	4.5	3.4	2.0	1.9	3.1
Cirsium vulgare		1.6				0.2
Sonchus arvensis	17.2	26.4	25.6	2.5*	19.2*	19.2*
Taraxacum officinale	2.2	3.6	4.1	11.6*	8.0*	11.3*

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[1] The FF treatment represents fall flooding.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Appendix XII: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of wet meadow zones associated with fall flooded wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Wet Meadow Zone associated with FF[1] Wetlands at Kitsim

Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre[2]	End	Post
	Canopy Cover (%)					
Native Species						
Alopecurus aequalis	1.1			0.2	0.3	0.3
Beckmannia syzigachne	3.4	1.7		2.7	2.2	2.3
Bouteloua gracilis					9.1	
Carex rostrata			0.3	2.8	3.0	2.5
Deschampsia caespitosa	2.9	2.5	1.6	3.3	1.4	1.4
Distichlis spicata				2.5	1.3	0.2
Eleocharis palustris	24.3	20.6	12.7	21.6	18.3	18.0*
Epilobium sp.					0.6	
Hippuris vulgaris	6.3			0.5		
Hordeum jubatum	7.2	5.2	3.4	7.0	7.3	13.3*
Juncus balticus	6.3	1.9	2.7	0.9*		
Mentha arvensis	0.5	2.5	3.4	5.0*	3.0	3.3
Plantago purshii.						0.2
Poa palustris	1.7	5.9	13.6	5.2*	5.2	8.3*
Polygonum sp.				0.3		
Puccinellia nuttalliana				0.8		0.2
Rumex occidentalis	2.4	7.2	6.1	8.8*	8.6	12.0*
Schizachne purpurascens	9.7	10.8	11.7	6.4	4.8*	9.2
Scirpus pungens	0.4		1.6		0.5	0.8
Introduced Species						
Chenopodium album		2.5	0.9	0.8	1.9	2.8
Cirsium arvense			1.3		0.2	0.2
Sonchus arvensis				1.0	3.8	2.2
Taraxacum officinale	0.2			0.3		
Typha latifolia	20.7	30.5	19.4	16.5	13.6*	12.5*

[1] The FF treatment represents fall flooding.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Appendix XIII: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of deep marsh zones associated with fall flooded wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Deep Marsh Zone associated with FF[1] Wetlands at Kitsim

Scientific Name	Ungrazed			grazed		
	Pre[2]	End	Post	Pre[2]	End	Post
	----------------	Canopy Cover (%)			----------------	
Native Species						
Eleocharis palustris				12.1		0.2
Hippuris vulgaris				1.3		
Hordeum jubatum						0.2
Rumex occidentalis			5.0			4.1
Schizachne purpurascens						2.5
Scirpus pungens				4.2		
Introduced Species						
Typha latifolia	95.0	95.0	95.0	72.5*	87.5	65.3*

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[1] The FF treatment represents fall flooding.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Appendix XIV: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of upland zones associated with spring flooded wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Upland Zone associated with SF[1] Wetlands at Kitsim

Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre[2]	End	Post
	-----Canopy Cover (%) -----					
Native Species						
Achillea millefolium	0.5	0.5	1.6	0.6	1.4	1.7
Agropyron smithii	43.0	27.0	31.3	29.5*	18.3*	21.3*
Agrostis scabra			0.5			
Antennaria parvifolia			0.2			
Artemisia cana			0.2	0.6		
Artemisia frigida	0.9	7.2	6.3	0.2	3.3*	7.0
Artemisia ludoviciana	2.5	0.8	1.1	3.6	0.8	
Bouteloua gracilis	0.3		0.2		0.3	
Carex filifolia	13.3	11.4	9.5	14.1	13.9	15.2*
Carex rostrata				3.0	2.5	
Carex sp.				0.2		3.1
Deschampsia caespitosa	0.2				0.8	0.3
Erigeron pumillus			0.2			0.2
Eleocharis palustris				0.5		
Gutierrezia sarothrae		0.2	0.8	0.3		0.2
Hordeum jubatum	5.0	5.6	5.3	1.7*	4.1	2.8*
Juncus balticus						0.2
Koeleria macrantha	2.0	1.7	0.8	4.4	2.0	1.1
Melilotus officinale			0.6			
Mentha arvensis	0.2	0.2	0.2			
Opuntia polyacantha			0.2	0.2		
Phlox hoodii		0.2				
Plantago purshii		0.3	0.2		0.3	
Poa palustris		0.3	0.3	1.4	4.2	4.7
Poa pratensis	6.9	6.9	4.7		6.6	2.2
Poa sandbergii						0.9
Polygonum sp.	0.3					
Ratibida columnifera	0.2		0.6	0.2		0.3
Rumex occidentalis	5.6	0.6	1.3	12.3*	0.8	0.6
Selaginella densa	3.1	1.6	0.2	6.4*	5.8*	7.8*
Solidago canadensis			0.3		0.2	0.2
Solidago sp.			0.3			
Sphaeralcea coccinea	0.3		0.2	0.6	0.3	0.3
Stipa comata	4.2	3.9	3.4	6.1*	0.5	5.8*

[1] The SF treatment represents spring flooding.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Appendix XIV (cont'd): Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of upland zones associated with spring flooded wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period (*P* < 0.05).

Upland Zone associated with SF[1] Wetlands at Kitsim						
Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre[2]	End	Post
	----------Canopy Cover (%) ----------					
Introduced Species						
Chenopodium album				0.5		
Cirsium arvense				2.7	3.9	4.5
Sonchus arvensis	2.5	2.0	1.4	0.6	5.3*	4.7
Taraxacum officinale		0.2	0.8	1.1	0.3	0.6
Thermopsis rhombifolia			0.2			
Tragopogon dubius	0.2					0.2

[1] The SF treatment represents spring flooding.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Appendix XV: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of dry meadow zones associated with spring flooded wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Dry Meadow Zone associated with SF[1] Wetlands at Kitsim

Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre[2]	End	Post
	----------------Canopy Cover (%)			---------------		
Native Species						
Achillea millefolium	0.5	1.9	1.1	0.8	0.9	0.8
Agropyron smithii	4.5	3.3	4.2	1.1	2.4	1.4
Agrostis scabra				0.2	0.2	0.2
Alopecurus aequalis						0.2
bareground					1.3	
Beckmannia syzigachne						1.3
Beckmannia syzigachne	0.3				0.2	
Carex atherodes	0.2	1.6	6.4			0.6*
Carex filifolia		0.3				
Carex rostrata	8.3	4.5	0.9	4.1*	3.9	0.6
Deschampsia caespitosa	12.0	8.9	1.7	5.8*	4.4*	0.8
Eleocharis palustris	5.3	2.2	0.8	1.4*	0.5	0.9
Epilobium sp.		0.3	0.5			
Erigeron sp.			0.2			
Gutierrezia sarothrae						0.2
Hordeum jubatum	10.5	12.0	3.1	10.3	20.2*	11.7*
Juncus balticus		1.6	1.1			
Melilotus alba	0.2					
Mentha arvensis	2.0	2.2	2.2	5.3*	1.7	2.5
Opuntia polyacantha			2.2			0.5
Poa palustris	12.7	7.3	14.5	16.9*	17.5*	18.1*
Poa pratensis	10.8	9.8	11.3	17.2*	10.0	13.4
Polygonum sp.	0.3			1.6		
Rumex occidentalis	10.5	1.9	1.4	12.7	4.2	0.5
Solidago canadensis	0.3	0.6	0.8		0.9	1.9
Introduced Species						
Chenopodium album	3.1	0.5	0.2	3.8	0.3	
Cirsium arvense	2.3	4.4	7.0	3.4	8.5*	10.2
Cirsium vulgare	2.7		0.3		0.3	0.6
Sonchus arvensis	0.9	19.7	23.8	1.7	9.6*	22.8
Taraxacum officinale	2.5	1.6	1.9	2.3	1.5	2.0

[1] The SF treatment represents spring flooding.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Appendix XVI: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of wet meadow zones associated with spring flooded wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Wet Meadow Zone associated with SF[1] Wetlands at Kitsim						
Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre[2]	End	Post
	Canopy Cover (%)					
Native Species						
Agropyron smithii			0.6			
Alopecurus aequalis		0.2	0.2			0.2
Beckmannia syzigachne	0.5	0.8	2.5	0.2	1.1	2.5
Carex rostrata	3.6	7.4	10.8		0.2*	1.4*
Deschampsia caespitosa	2.3	2.0	0.9	3.4	1.6	6.1
Eleocharis palustris	23.1	11.9	9.2	19.8	12.7	5.0*
Epilobium sp.		1.9			0.2	
Hordeum jubatum	4.8	13.9	8.9	12.7*	19.4*	20.8*
Lappula sp.						0.8
Lycopus sp.						0.2
Mentha arvensis	0.3		0.2	0.3	0.6	
Opuntia polyacantha			5.9			1.1*
Poa palustris	3.1	1.4	6.4	1.1	5.2*	15.0*
Poa pratensis						0.2
Polygonum sp.		0.3	0.5	0.5	1.9	
Potentilla sp.		0.3	0.3			1.4
Rumex occidentalis	32.0	26.4	6.3	39.8*	37.2*	6.9
Schizachne purpurascens	0.8	0.3	1.9	1.9	1.6	10.6*
Introduced Species						
Chenopodium album	3.4	13.2		9.4*	6.6*	1.7
Cirsium arvense	0.5	1.9	4.8	0.2	1.6	7.7
Cirsium vulgare						0.3
Sonchus arvensis		4.3	12.3		4.5	9.2
Taraxacum officinale		0.3		0.5		0.3
Typha latifolia	18.0	9.7	18.9	2.2*	4.1*	4.4*

[1] The SF treatment represents spring flooding.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

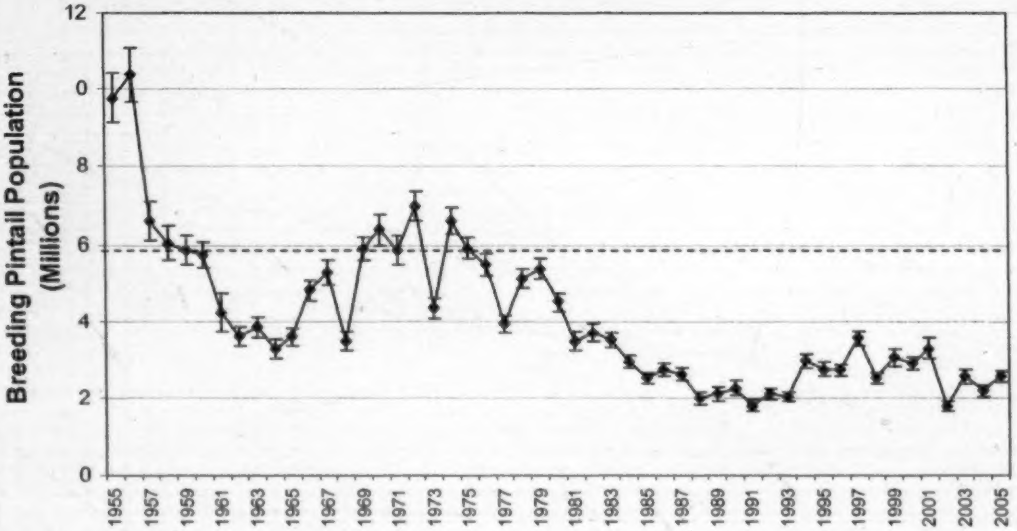
Appendix XVII: Vegetation (native and introduced species) composition and relative abundance (canopy cover) in ungrazed and grazed areas of deep marsh zones associated with spring flooded wetlands at Kitsim. For species with at least, 5% cover value in any of the three sampling periods (i.e., Pre, End and Post), grazed plant cover marked by an asterisk differ from the ungrazed value within the same sampling period ($P < 0.05$).

Deep Marsh Zone associated with SF[1] Wetlands at Kitsim						
Scientific Name	Ungrazed			Grazed		
	Pre[2]	End	Post	Pre[2]	End	Post
	Canopy Cover (%)					
Native Species						
Beckmannia syzigachne					0.3	
Carex rostrata		2.5				
Eleocharis palustris	10.0	6.3		19.6*	5.0	
Hordeum jubatum				2.5	2.7	
Juncus balticus				1.3		
Rumex occidentalis	1.3	13.8		2.5	5.8*	
Schizachne purpurascens	1.3	7.5		0.4	2.5	
Introduced Species						
Chenopodium album				1.7		
Sonchus arvensis		1.3				
Typha latifolia	87.5	68.8	100.0	72.1*	63.6	100.0

[1] The SF treatment represents spring flooding.

[2] Pre, End and Post represent pre-treatment, end-of-treatment, and post-treatment reflooding sampling periods

Appendix XVIII: Fifty-year trend (1955 – 2005) in the population of breeding Pintails in the Prairies. Dashed line indicates the current Pintail population management goal of the North American Waterfowl Management Plan (NAWMP).



Appendix XIX: List of breeding waterfowl species encountered during census on study wetlands at Contra-Costa and Kitsim from May 2003 to May 2005.

Species	Contra-Costa	Kitsim
American Wigeon	X	X
Blue-winged Teal	X	X
Bufflehead	X	X
Canada Goose	X	X
Canvasback	-	X
Cinnamon Teal	X	X
Gadwall	X	X
Lesser Scaup	X	X
Mallard	X	X
Northern Pintail	X	X
Northern Shoveller	X	X
Redhead	X	X
Ruddy Duck	X	X

Appendix XX: Incidental waterfowl nests encountered at Contra-Costa and Kitsim from 2003 to 2005.

Study Year	Date Sighted	Waterfowl Species	Nest Size	UTM Easting	UTM Northing	Nest Habitat	Nest Fate	Cause	Remark
Contra-Costa									
2003	May. 12	CAGO	8	467665	5583399	grassland	abandoned	unknown	not successful
2003	May. 27	GADW	7	467503	5583593	grassland	destroyed	predation	not successful
2004	May. 03	BWTE	10			grassland	destroyed	investigator damage	not successful
2004	May. 15	NOSH	1			grassland	unknown		investigator ended survey
2004	May. 16	NOPI	7	468930	5583569	grassland	unknown		investigator ended survey
2004	May. 27	NOSH	5			grassland	unknown		investigator ended survey
2004	May. 29	BWTE	7	466569	5587409	grassland	unknown		investigator ended survey
2005	Jun. 27	NOPI	6	468799	5583773	grassland	destroyed	predation	not successful
Kitsim									
2003	May. 14	MALL	2	419489	5594310	grassland	destroyed	predation	not successful
2003	May. 15	MALL	14	426081	5597253	wetland	abandoned	investigator disturbance	not successful
2003	May. 15	CAGO	5	422057	5594771	grassland	hatched		successful
2003	May. 30	MALL	6	426272	5595521	grassland	destroyed	predation	not successful
2003	Jun. 19	GADW	9	426228	5594749	grassland	hatched		successful
2003	Jul. 05	REDH	22	419593	5593839	wetland	unknown		investigator ended survey
2004	May. 02	CAGO	3			grassland	destroyed	predation	not successful
2004	May. 16	NOSH	10	425703	5594952	grassland	unknown		investigator ended survey
2004	May. 16	NOSH	10	421978	5594706	grassland	destroyed	predation	not successful
2004	May. 28	MALL	6			grassland	unknown		investigator ended survey
2004	Jul. 06	GWTE	9	425233	5597087	grassland	hatched		successful
2005	May. 11	NOPI	3	426292	5595241	grassland	unknown	unknown	investigator ended survey
2005	May. 11	NOPI	4	421658	5595805	grassland	destroyed	predation	not successful
2005	Jun. 29	BWTE	8	425720	5594883	wetland	hatched		successful
2005	Jun. 29	BWTE	1	425249	5597078	grassland	destroyed	predation	not successful
2005	Jul. 12	GADW	6	421164	5595772	grassland	destroyed	predation	not successful

Appendix XXI: Incidental waterfowl broods encountered at Contra-Costa from 2003 to 2005.

Date	Time	Species	Brood Size	Age Class
4-Jul-03	8:48	NOSH	13	2B
4-Jul-03	9:05	NOPI	4	2B
4-Jul-03	9:05	NOPI	6	2C
4-Jul-03	9:05	NOPI	3	1C
4-Jul-03	9:17	NOSH	5	2A
4-Jul-03	9:17	NOSH	9	2A
4-Jul-03	9:17	NOPI	8	2A
4-Jul-03	9:17	NOPI	4	2A
4-Jul-03	9:17	BWTE	6	1C
4-Jul-03	10:03	GADW	8	2B
4-Jul-03	10:03	GADW	14	1C
4-Jul-03	10:03	GADW	9	1C
4-Jul-03	10:09	BWTE	1	1A
4-Jul-03	10:09	NOPI	16	2C
4-Jul-03	10:14	AMWI	8	1A
4-Jul-03	10:14	NOPI	7	2B
4-Jul-03	10:14	GADW	9	1A
4-Jul-03	10:26	NOSH	7	1C
4-Jul-03	10:51	AMWI	11	1A
4-Jul-03	10:51	BWTE	14	1B
4-Jul-03	10:51	NOSH	13	1C
4-Jul-03	10:51	REDH	6	1B
4-Jul-03	10:51	AMWI	10	1C
4-Jul-03	10:51	AMWI	8	1C
11-Jun-03	12:15	CAGO	2	2A
18-Jun-03	9:15	NOPI	7	1B
18-Jun-03	9:15	NOPI	3	1B
18-Jun-03	8:30	NOSH	7	1B
18-Jun-03	11:22	NOSH	8	1B
20-Jun-03	13:50	NOSH	3	1B
20-Jun-03	14:00	NOPI	4	2A
13-May-04	8:08	NOPI	4	1A
14-May-04	7:05	NOPI	6	1A
14-May-04	7:12	NOPI	3	1A
14-May-04	7:12	NOPI	4	1A
14-May-04	7:12	CAGO	4	1A
16-May-04	15:15	NOPI	3	1A
28-May-04	7:54	NOPI	3	1C
28-May-04	7:54	NOPI	2	1C
28-May-04	8:14	NOPI	11	1B
28-May-04	16:10	NOSH	11	1B
27-Jun-05	8:30	BWTE	4	1B
27-Jun-05	9:50	NOPI	4	1C
13-Jul-05	8:30	BWTE	2	1B
13-Jul-05	9:18	BWTE	7	1B
14-Jul-05	10:35	COOT	3	1A

Appendix XXII: Incidental waterfowl broods encountered at Kitsim from 2003 to 2005.

Date	Time	Species	Brood Size	Age Class
14-May-03	10:00	CAGO	7	1A
15-May-03	9:45	CAGO	7	1A
15-May-03	10:15	CAGO	2	1B
29-May-03	8:00	CAGO	4	1B
29-May-03	8:45	CAGO	3	2B
31-May-03	11:25	CAGO	6	1B
10-Jun-03	14:25	CAGO	7	2B
10-Jun-03	14:25	CAGO	3	2B
10-Jun-03	14:30	CAGO	10	2A
10-Jun-03	14:31	CAGO	3	1C
10-Jun-03	14:35	CAGO	6	1A
20-Jun-03	9:10	NOPI	6	1B
14-May-04	10:07	CAGO	5	1A
15-May-04	11:00	CAGO	5	1A
15-May-04	11:00	CAGO	4	1A
16-May-04	8:24	CAGO	2	1A
16-May-04	7:05	CAGO	7	1A
27-May-04	9:16	CAGO	5	1B
28-May-04	9:16	CAGO	8	2A
28-May-04	9:16	CAGO	6	2A
28-May-04	9:16	CAGO	5	2A
28-May-04	10:26	CAGO	6	1C
28-May-04	10:26	CAGO	6	1A
28-May-04	10:26	CAGO	9	1A
28-May-04	10:26	CAGO	3	1B
28-May-04	10:26	CAGO	2	1B
26-May-05	10:40	NOPI	5	1A
11-Jul-05	12:45	CAGO	8	3
11-Jul-05	12:45	CAGO	3	3
12-Jul-05	8:23	NOPI	3	2C
12-Jul-05	8:23	CAGO	6	3
12-Jul-05	8:23	CAGO	9	3
12-Jul-05	8:23	CAGO	6	3
12-Jul-05	8:23	GADW	2	2C
12-Jul-05	8:23	BWTE	11	2C
12-Jul-05	8:23	BWTE	11	1C
12-Jul-05	10:24	NOPI	6	3
20-Jul-05	9:34	GADW	7	1C
20-Jul-05	9:34	GADW	4	1C
20-Jul-05	9:34	GADW	7	1B
20-Jul-05	9:47	NOPI	5	2C
20-Jul-05	10:40	GADW	4	1B

Appendix XXIII: Waterfowl predator encounter rates at Contra-Costa and Kitsim during waterfowl survey in May of 2003, 2004 and 2005.

Waterfowl Predator	Encounter Rate /Hour		
	2003	2004	2005
Contra-Costa			
Coyote		0.3	0.3
Crow			1.7
Large Gull	2.4	0.5	0.4
Northern Harrier	0.8	1.0	0.5
Raven			0.7
Red-tailed Hawk	0.3		
Short-eared Owl		0.6	
Swainson's Hawk	0.4	0.7	0.2
Kitsim			
Coyote	0.3	0.3	0.3
Crow	0.6	0.3	0.3
Large Gull	3.6	2.3	4.6
Shrew /Voles	0.3		
Northern Harrier	0.5	0.9	0.6
Red-tailed Hawk	0.9		
Short-eared Owl	0.5		0.3
Swainson's Hawk	0.8	0.4	0.3
Unknown Hawk	0.3		0.3
Weasel		0.3	

Appendix XXIV: List of other wildlife species encountered at Contra-Costa and Kitsim from August 2002 to October 2005.

Contra-Costa	Kitsim
List of Mammals	
Coyote	Badger
Elk (Wapiti)	Coyote
Jack Rabbit	Jack Rabbit
Mule Deer	Lesser Weasel
Pronghorn	Long-tailed Weasel
Richardson's Ground Squirrel	Mule Deer
White-tailed Deer	Pronghorn
	Richardson's Ground Squirrel
	White-tailed Deer
List of Birds	
America Avocet	American Avocet
Barn Swallow	American Kestrel
Black Tern	American White Pelican
Black-capped Night Heron	Barn Swallow
Black-necked Stilt	Black Tern
Brewer's Blackbird	Black-necked Stilt
Brown-headed Cowbird	Brewer's Blackbird
California Gull	Brown-headed Cowbird
Chestnut-collared Longspur	California Gull
Common Crackle	Chestnut-collared Longspur
Common Tern	Common Tern
Eastern Kingbird	European Starling
Franklin's Gull	Forster's Tern
Horned Grebe	Franklin's Gull
Horned Lark	Horned Grebe
House Sparrow	Killdeer
Killdeer	Lark Sparrow
Lark Sparrow	Marbled Godwit
Least Sandpiper	Marsh (Northern) Harrier
Marbled Godwit	Mountain Plover
Marsh Harrier	Red-winged Blackbird
Mountain Plover	Swift
Red-winged Blackbird	Upland Sandpiper
Swainson's Hawk	Western Meadowlark
Western Meadowlark	Yellow Warbler
Wilson's Phalarope	Yellow-headed Blackbird
Yellow-headed Blackbird	
List of Reptiles and Amphibians	
Leopard Frog	Plains (Prairie) Garter Snake
Boreal Chorus Frog	

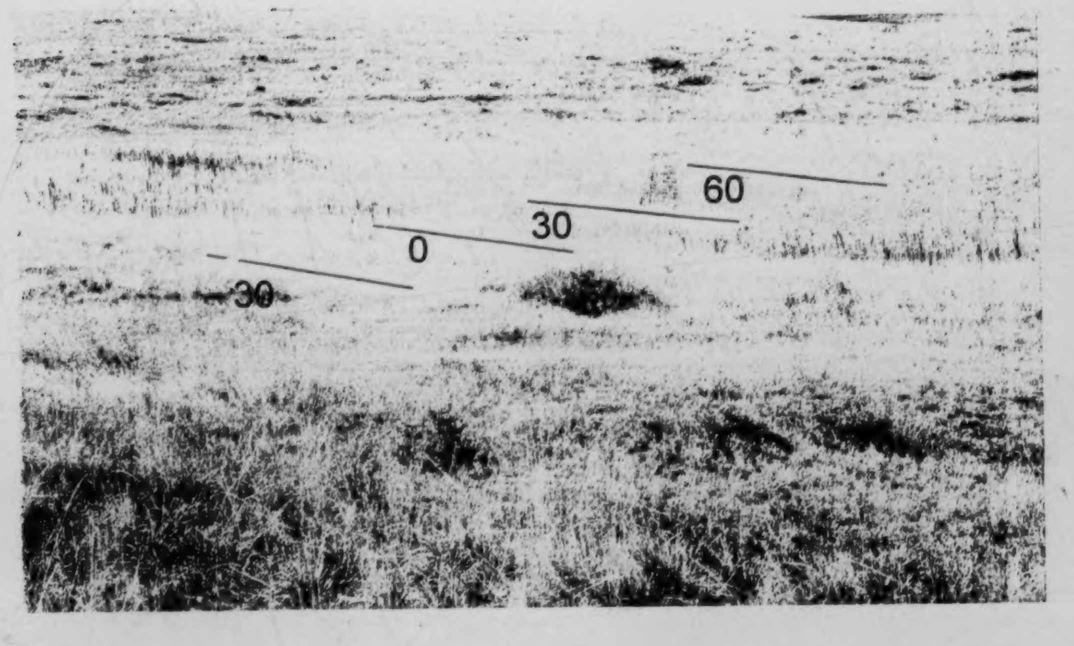
Appendix XXV: *E. palustris* is the desirable plant community (DPC) that develops with initial shallow artificial flooding of meadows in Dry Mixed Grass Prairie rangelands of southeastern Alberta, Canada. Extended deep flooding leads to competitive displacement of *E. palustris* by *T. latifolia*.

Appendix XXVI: *T. latifolia* is the plant community that has displaced spikerush from wetlands created by Ducks Unlimited Canada (DUC) in the Dry Mixed Grass Prairie in the last 20 years. Although cattle may occasionally feed on it, *T. latifolia* invasion defeats the objective of enhancing spikerush abundance in the region. Grazing exclosures facilitated the quantification of moisture treatment effects under grazed and ungrazed conditions at Kitsim.

Appendix XXVII: Grazing and trampling may reduce *T. latifolia* abundance and vigor on created wetlands exposed to cattle grazing in the Dry Mixed Grass Prairie.

Appendix XXVIII: Wetlands in the Dry Mixed Grass Prairie are flooded using a gravity-fed irrigation canal system regulated by flood control structures (not in photograph).

Appendix XXIX: Typical study wetland at Contra-Costa showing locations of permanent transects in four topographic positions, including sub-irrigated uplands (-30 cm), waterline (0 cm), shallow (30 cm) and deep (60 cm) flooding zones on the landscape



Appendix XXX: Contra-Costa wetlands were annually flooded until target depths were achieved. Use of range cages enabled the assessment of moisture effects under grazed and ungrazed conditions across topographic positions at Contra-Costa.